Chapter 1

Introduction

1.1 Introduction

This thesis is about the ecology and behaviour of feral pigs *Sus scrofa* (L.) and how this ecology and behaviour may influence the epidemiology of an exotic livestock disease, foot and mouth disease (FMD). As such the thesis is divided into two main parts. The first is an empirical study of the ecology of feral pigs in terms of the effect of food availability and temperature on the habitat use, home range size, distance moved, and body weight of a population at Nocoleche Nature Reserve north-west New South Wales. This section also includes a test of the influence of feral sows in oestrus on the movements of feral boars. The second part of the thesis takes behavioural data collected from the Nocoleche pig population on contact rates between pigs and movement rates of individual pigs, plus demographic data on feral pigs from other studies to build a model of FMD in feral pigs in the semi-arid rangelands. This model predicts the mean persistence time of an FMD outbreak, threshold density of pigs below which the disease will not persist, and rate of spread of the disease.

The abiding theme running through this thesis is how changes in an unpredictable environment influence the behaviour and ecology of an introduced adaptable ungulate and how hypothetically this variability may influence the behaviour of an FMD epizootic.

1.2 The Ecology and Behaviour of Wild Pigs

Feral pigs are the most widely introduced large mammal, being found in Australia, the United States, New Zealand, South America as well as numerous Pacific and Caribbean islands (Lever 1985). The wild boar (the original wild form of *Sus scrofa)* also enjoys a wide distribution being found throughout Europe and Asia except the far north, as well as north Africa. This suggests that wild pigs are highly adaptable animals. In Australia they are found in a variety of habitats including alpine (Saunders 1993), monsoon savanna (Hone 1990), montane forest (Saunders & Kay 1990), rainforest (McIlroy 1993) and semi-arid rangeland (Giles 1980).

Pigs are omnivorous as is the ecologically similar bush pig *Potamochoerus porcus* (Skinner *et al.* 1976). Compared to other artiodactyls, suids lack complex physiological adaptations for herbivory. Warthogs *Phacochoerus aethiopicus* however, are grazers with lophodont dentition (Ewer 1958, Eisenberg 1981) but most suids have simple bunodont dentition and unilocular stomach and a relatively small caecum (Eisenberg 1981). They are capable of only limited hind gut digestion of cellulose (Cranwell 1968) which means they can not live entirely off low quality vegetation like herbivores can with complex digestive systems.

The diet of pigs is well documented from a variety of locations. The diets show strong seasonal and regional variation in the importance of various food types. A feature of the diets of pigs in temperate North America and Europe is their strong seasonal dependence on mast fruiting of oaks *Quercus* spp. (Oloff 1951, Barrett 1978, Wood & Roark 1980, Genov 1981, Baber & Coblentz 1987). Mast is a very high energy food source (Barrett 1978) and such is the dependence of pigs on mast that body condition and fecundity are predictable from the size of the mast crop. This contrasts with a dependence on fresh grass and forbs in tropical, semi-arid, and island habitats (Griffin 1978, Giles 1980, Pavlov 1980, Coblentz & Baber 1987). The pasture consumed is almost always fresh (Barrett 1978, Giles 1980) with succulent plants being particularly preferred (Giles 1980, Baber & Coblentz 1987). Like mast, the amount of available pasture in the semi-arid region is a predictor of body condition and fecundity (Giles 1980). Roots of woody plants are eaten, but only when other foods are less readily available (Giles 1980, Wood & Roark 1980).

A persistent feature of all diet studies is the presence of small amounts of carrion and invertebrates (Oloff 1951, Hoogerwerf 1970, Challies 1975, Barrett 1978, Griffin 1978, Giles 1980, Pavlov 1980, Wood & Roark 1980, Genov 1981, Baber & Coblentz 1987, Coblentz & Baber 1987). In some cases invertebrates such as crabs can dominate the gut content of individual pigs (Diong 1973). Pigs may also kill and eat new-born vertebrates as large as lambs (Pavlov *et al.* 1981).

Along with their omnivory two other aspects of pig physiology may contribute to their successful establishment in a variety of habitats. This is their response to high fibre diets and their very low metabolic rate. As stated pigs have a limited ability to digest cellulose but they can respond to high fibre diets by increasing food intake (Frank *et al* 1983) and increasing the rate food passes through the gut (King & Taverner 1975), in contrast to ruminants which decrease their food intake and rate of passage with increasing dietary fibre content (Janis 1976). This could give pigs the same advantage over ruminants that Janis (1976) postulates for equids. That is, when environmental conditions deteriorate and the fibre content of available vegetation is high, pigs are not locked into a damaging positive feedback with high fibre food slowing the digestion as in ruminants.

The second physiological trait is the very low metabolic rate (0.11 O_2/hr/g) in comparison to all other mammals (Eisenberg 1981). The lower the metabolic rate, the lower the energetic requirements and the greater the resistance to starvation. Thus although high quality foods for pigs may be temporally patchy, pigs can endure longer between meals than other artiodactyls because of their low metabolic rate.

Young pigs are weaned at approximately two months of age (Giles 1980). Female European wild boar breed when they reach a critical body weight of 40 kg (Pepin *et* *al.* 1987). Feral pigs in north-west New South Wales breed at 20-25 kg for sows under 18 months old and 25-30 kg for sows over 18 months old, (Giles 1980).

The timing of birth or "farrowing" in wild pigs is under the control of both photoperiod and food supply. Mauget (1982) established that for European wild boar, conception was associated with declining photoperiod. However, the actual commencement of breeding was influenced by the availability of food. In tropical Asian wild boar, reproduction is synchronised but the breeding season varies regionally; - different part of Java having different breeding seasons (Hoogerwerf 1970). Sweeney *et al.* (1979) found a mid-winter peak in farrowing by feral pigs in subtropical Georgia but some farrowing occurred in all seasons. In central California feral pigs had a late autumn farrowing peak (Barrett 1978). In an island off southern California Baber & Coblentz (1986) noted a change in farrowing peak from winter-spring to spring-summer between years and attributed the differences to variation in the abundance of the mast crop. Feral pigs on the equatorial Galapagos Islands breed aseasonally (Coblentz & Baber 1987), as do feral pigs in the semi-arid rangelands of Australia (Giles 1980). In sub-alpine New South Wales, Saunders (1993) found a summer peak in farrowing and ascribed the difference between those pigs and pigs of northern hemisphere temperate regions as being due to a summer food peak in sub-alpine areas and the lack of an autumn mast crop in Australia. The variation in timing and synchrony of reproduction in wild pigs shows their reproductive physiology is able to override any synchronising effect of photoperiod to give birth at the most favourable time for the nutrition of piglets.

Suids are unusual amongst artiodactyls in having multiple births. Only the related peccaries and Chinese water deer *Hydroptes inermis* give birth to litters (Eisenberg 1981). Compared to herbivores of similar size this gives suids a very high potential rate of increase.

The litter size for wild boar does not vary much over the species geographic range, being 4.6 in France (Mauget 1981), 5.0 in Germany (Oloff 1951), and 4.5 in Malaysia (Diong 1973). Estimates of feral pig litter size are 5.0 for Santa Catalina Island, California (Baber & Coblentz 1986), 4.7 for the Galapagos Islands (Coblentz & Baber 1987) and from 5.6 to 6.9 in north-western New South Wales (Giles 1980). Comparisons between these estimates need to be treated with caution as litter size was measured in some of these studies by the number of foetuses (without specifying the stage of pregnancy) while others were from counts of new born. Domestic pigs have a much higher litter size than feral pigs, ranging between 9 to 14 (Hagen & Kephart 1980).

Mauget (1981) described the basic social units of wild pigs as females and young frequently in association with other females and their young. Young of the previous year, both male and female, may be loosely associated with these female groups (Gundlach 1968). Males over three years old are solitary. Wild pigs are non-territorial and promiscuous (Frädrich 1974, Graves 1984). This social organisation contrasts with other suids such as the warthog which is both monogamous and territorial (Frädrich 1974) and the bush pig which is monogamous (Skinner *et al.* 1976).

The home ranges of pigs tend to contain several common features. These are dense cover, free water, wallows, and rubbing places such as particular stones and trees (Stegeman 1938, Frädrich 1974, Graves 1984). Most researchers stress the importance of cover in protecting pigs from the sun as pigs are known to be very sensitive to heat stress (Mount 1968). Cover is not only important for shelter from extreme weather but because pigs have extended sleep periods compared to ruminants (Frädrich 1974) they need to be concealed for prolonged periods. Water and more particularly mud to wallow in is also believed to be very important in allowing pigs to evaporatively cool. As pigs have a short neck and relatively inflexible build and can not reach much of their body with their mouth, in grooming the skin rubbing places are important.

Feral sows (while not pregnant) come into oestrus every 20 days and oestrus normally lasts up to four days (Kilgour & Choquenot 1994). Oestrus is characterised by restless behaviour in domestic sows (Hafez & Signoret 1969). Males are believed to respond principally to behavioural cues in determining a sow's sexual status, although females in oestrus are attracted to boars (Signoret 1970). The following description of courtship and mating behaviour comes from Hafez & Signoret's (1969) review of the behaviour of pigs. Courtship consists of sniffing the genitalia by both sexes and head to head nuzzling and the production of a rhythmic series of soft grunts by the boar. The male may then nose the flanks before the female adopts the mating stance, a rigid stance with back arched and limbs locked. Once this position is elicited the boar mounts and copulation commences, which may last from three to 20 minutes.

Fighting between boars is known in wild pigs (Gundlach 1968, Barrett 1978, Barrette 1986) and domestic pigs (Hafez & Signoret 1969, Fraser 1984). Fighting has also been observed in wild sows (Barrette 1986). The sequence of behaviour leading up to fighting in adult male wild boar has been described by Gundlach (1968)as starting with one combatant approaching the other with head lowered and back bristles of both animals erect. They then align themselves parallel to one another before moving closer with heads raised. One animal will then stand broadside in front of the other. This is followed by head to head and head to shoulder confrontation where the animals try to push and shove one another, especially by pushing under the groin. Gundlach (1968) does not mention any variations in the behaviour or its sequence though Barrette (1986) observed wrestling between adult boars in Sri Lanka, with both sets of forefeet off the ground. Frädrich (1974) noted warthogs engage in a more ritualised head to head confrontation.

Skinner *et al.* (1976) mentions similar fighting behaviour in bush pigs with the additional behaviour that males may roll in dust before a fight.

Males have been observed fighting over access to females (Barrett 1978, McIlroy 1989). Barrett observed fighting in groups of up to 10 males gathered around an oestrous sow. One boar usually dominated mating while other boars fought, or attempted to mate with the head of the sow or each other. Less dominant boars often retreated before the lowered head, erect back bristle approach of a more dominant boar. Herring (1972) speculates that in comparison to the short dagger like, non-sexually dimorphic canines of peccaries which are adapted for defence, the sharp, outward pointing lower canines and the upward pointing upper canines of male suids are evolved for contests between males over access to females.

In both domestic pigs (Jensen *et al* 1987) and feral pigs (Kurz & Marchinton 1972) females become restless before birth and separate themselves from other pigs. Pigs are unique amongst artiodactyls in building nests for giving birth (Gundlach 1968). This nest is constructed several days prior to farrowing and consists of an oval shaped depression slightly larger than the body of the sow and filled with twigs, grass and branches. This pile of vegetation is hollowed out by the sow and it is within this nest that she gives birth. The most probable reason for building a nest is that the young of pigs despite being semi-precocial have little ability to thermoregulate for the first few days of life (Gundlach 1968, Fraser 1984). Nest building occurs throughout the wild pigs, range including the tropics (Diong 1973). In their multiparity, nest building and semi-precocial young, pigs more closely resemble some rodents rather than other artiodactyls (Gundlach 1968).

Sows give birth lying on their side and may give the piglets some assistance in moving to the teats (Hafez & Signoret 1969). Both domestic sows (Jensen 1986) and wild boar sows (Gundlach 1968) stay close to the nest for about nine days before leaving with the piglets.

1.3 Wild Pig Management

Wild pigs represent both an economic resource and an economic and environmental liability. These different perceptions of their status vary within and between communities and can lead to conflicts over what is the most appropriate management strategy (Tisdell 1982, O'Brien 1987). Throughout much of their range they are hunted for sport and food. In much of Europe they are intensively managed with supplementary feeding to provide adequate game for sport shooters (Andrzejewski & Jezierski 1978). In Australia they are hunted both for recreation and for export as game meat (O'Brien & Meek 1992). In America, European wild boar were deliberately introduced to North Carolina and California as game animals. These boar spread from their original sites of introduction interbreeding with the existing population of feral pigs (Pine & Gerdes 1973). In Australia the appearance of small populations of feral pigs far from their main centres of distribution has been blamed on recreational hunters trying to establish pig populations closer to home (Wilson *et al.* 1991).

Introduced populations of wild pigs have been identified as an environmental threat in a number of localities. Damage is usually associated with wild pigs propensity to root up soft ground in search of tubers and invertebrates. In the Great Smokey Mountains of the south-east United States, wild boar have removed much of the herbaceous ground cover of deciduous forests (Bratton 1975). In Hawaii Volcanoes National Park, Hawaii, feral pigs severely reduced the cover of ferns through their extensive rooting (Griffin 1978) while on Auckland Island off southern New Zealand, feral pigs almost eliminated three species of herbaceous plant (Challies 1975). The impact of feral pigs on animals is less well known, although predation by feral pigs was shown to be the main cause of the decline in abundance of the Lord

Howe Island woodhen *Tricholimnus sylvestris* on Lord Howe Island in the South Pacific (Miller & Mullette 1985). In the Galapagos Islands, Ecuador, feral pigs are believed to have contributed to the decline in a number of endemic reptiles through nest predation (Coblentz & Baber 1987). Pigs have also been implicated in the decline of the cassowary *Casuarius casuarius* in north-east Queensland (Crome & Moore 1990). In summary pigs represent a threat to the herbaceous plants through their extensive rooting and to ground nesting birds and reptiles through predation.

The main management concern with wild pigs in several countries is as a pest of agriculture. In Poland they are known to destroy up to 46.7%, 13.7%, and 37.4% of rye, oats, and potato crops, respectively (Andrzejewski & Jezierski 1978) while in Malaysia wild pigs can destroy whole tapioca crops (Diong 1973). In the Northern Territory of Australia, Cayley (1993) showed that a 76% reduction in feral pig numbers could reduce damage to sorghum and maize crops by 71%. In Australia in 1980 total damage to the economy was put at $75 million (Tisdell 1984). The main management concern with feral pigs in Australia has been their impact on wool production through predation on new born lambs (Plant *et al.* 1978, Pavlov *et al.* 1981). Estimates of losses range from 1.6% to 37.9% of lambs born (Pavlov *et al.* 1981).

Feral pigs in Australia are reservoirs for a number of endemic diseases. The diseases of most concern to human and animal health are leptospirosis *Leptospira* spp., Porcine brucellosis *Brucella suis*, meliodosis *Pseudomonas pseudomallei*, and tuberculosis *Mycobacterium* spp. (Korn *et al.* 1994). Leptospirosis, and meliodosis can be contracted through skin abrasions and orally when handling feral pigs (Korn *et al.* 1994). Both are serious diseases of humans with meliodosis sometimes being fatal. Porcine brucellosis is also a serious human disease and its incidence in Queensland is strongly correlated with people who have a history of hunting feral pigs (Robson *et al.* 1993). Bovine tuberculosis is common in pigs in the Northern

Territory and it is assumed the main route for infection of these animals is through eating contaminated cattle and water buffalo *Bubalus bubalis* carcasses (Corner *et al.* 1981). Pigs do not readily transmit any form of tuberculosis and are therefore not regarded as a major host in the transmission of the disease (Corner *et al.* 1981). A further risk to human health is through ingestion of the larvae of the cestode *Spirometra erinacei* (sparganosis) through eating under cooked pork meat (Pavlov 1990).

Perhaps a greater threat than that posed by endemic diseases, crop damage, and lamb predation is threat of exotic wildlife disease becoming established in feral pigs in Australia. The potential threat posed by these animals as reservoirs of FMD, rinderpest, classical swine fever and African swine fever has been recognised for some time (Pullar 1950). The disease that has received the most attention is FMD because it is highly infectious, causes serious productivity loss, and would ensure closure of access to the lucrative North American and Japanese meat markets for Australian livestock products (Wilson & O'Brien 1989).

1.4 The Ecology of Diseases

Parasites and the diseases associated with them, have had a pervasive influence on the physiology, ecology and evolution of multicellular organisms (Anderson & May 1982). This influence goes beyond the evolution of complex immune systems to the evolution of social groupings (Freeland 1979), brilliant colours and ornaments (Hamilton & Zuk 1982) and even sex itself (Hamilton 1980). Parasites and the diseases associated with them have also had a powerful influence on human history with infectious disease being the major source of mortality throughout much of human history (McNeil 1976). Despite the importance of the diseases relatively little is known of the epidemiology of diseases in wild populations of animals (Plowright 1988). Where attention has been paid to the dynamics of wild animal diseases it is usually because the diseases are of concern to human health such as rabies in red foxes *Vulpes vulpes* (Anderson *et al.* 1981) or to the health of domestic animals such as bovine tuberculosis in badgers *Meles meles* (Anderson & Trewhella 1985) and brush-tailed possums *Trichosurus vulpecula* (Barlow 1991) or the control of a pest species such as rabbits *Oryctolagus cuniculus* with Myxomatosis (Fenner & Ratcliffe 1965). This is understandable given the difficulty in detecting many diseases without elaborate laboratory tests. However a growing body of evidence is pointing to the importance of diseases as regulators of wild animal populations (May 1983, Plowright 1988). The following paragraphs outline some of the more important aspects of disease models and how they may regulate animal populations.

For epidemiological purposes it is convenient to think of disease agents in two categories; microparasites and macroparasites (Anderson & May 1979). Microparasites are viruses, bacteria, protozoa, and fungi while macroparasites are helminthes and arthropods. Microparasites are small and with some exceptions tend to infect the host for a relatively short period, they usually reproduce within the host at a very high rate. If hosts recover from a microparasitic infection they acquire temporary or lifelong immunity depending upon the disease although some individuals may have carrier status, spreading the parasite without showing symptoms of the disease. Macroparasites, are larger with much longer generation time than microparasites. The immune response to macroparasites is dependent on the number of parasites and is only of short duration if the parasites are removed. The distribution of macroparasites within a host and between hosts is very clumped. This means that a host can be infected without showing symptoms of a disease. With microparasitic infections the host is either infected with the disease and usually shows symptoms of the disease or is uninfected. Some diseases are synergistic combinations of a microparasite and a macroparasite such as the lungworm-pneumonia complex in bighorn sheep *Ovis canadensis* (Forrester 1971).

When an animal catches a microparasitic infection it passes through several discrete disease states. These states are susceptible, infective, and immune. Susceptibles are those individuals who have never been exposed to the disease. Infectives are those who were susceptible but now have the disease and are spreading the disease. Immunes are those who have had the disease and now have temporary or permanent immunity. If immunity is transitory then immunes will return to being susceptible. A fourth category latents may occur between susceptibles and infectives. Hosts that are latent have been colonised by the microparasite but are not yet infectious. These discrete states make the dynamics of microparasitic infections amenable to categorical modelling, where a series of differential equations describing the rates at which hosts pass through particular states, are linked together to describe the dynamics of the disease. There are several important parameters governing the rate at which individuals pass through these disease categories are represented in Figure 1.1. The parameters a and b are simply the birth rate of the host population respectively. The parameter β is the transmission coefficient and governs the rate at which susceptibles become infectives. This parameter is one of the most complex and difficult to measure. β is composed of the infectiousness of the disease a function of how many microparasites are produced, how long they survive, and how they are transmitted to the host. It is also dependent on the behaviour and physiology of the host, its susceptibility to infection, and how close and how often it comes in contact with other hosts. The rates at which a host passes from latent to susceptible σ, from infectious to immune υ, and immune to susceptible ω, are constants set by the physiology of the disease and the host. The disease related mortality rate α depends on the type of the disease and its strain and the type of host infected as well as the physical condition of the host and its age.

Critical to the probability of an epidemic establishing itself in a population of hosts is the parameter R_0 (May 1983, Mollison 1987). For microparasites R_0 is the average number of secondary infections produced when a single infected individual is introduced into a susceptible host population (May 1983). For the disease to persist R_0 must be greater than unity. R_0 itself is dependent on the number of susceptible hosts available with the higher the number of susceptible hosts the higher R_0. The dependence of R_0 on abundance of hosts leads to the concept of N_T, this is the threshold abundance of susceptible hosts above which R_0 is positive and the disease will persist and below which R_0 is negative and the disease will not persist. This means that in general, the higher population size the more likely a disease is to persist. Sexually transmitted diseases are exceptions to this in that R_0 depends upon the rate at which new sexual partners are acquired rather than the abundance of the hosts (May 1983).

The dynamics of a disease once it is established in a population will usually become either endemic and persist at a usually low stable prevalence, or epidemic and outbreak at high levels of prevalence, either regularly or irregularly (May 1981). Purported examples of cyclical changes in density due to an epidemic are the nine to ten year cycle of the larch budmoth *Zeiraphera diniana* populations in Switzerland, infected with a granulosis virus, and the three to five year cycle of fox populations infected with rabies in Europe (May 1983).

The disease models described so far are simplistic in that they do not include the effect of spatial heterogeneity in disease transmission (Anderson & May 1991). This lack of uniformity in disease transmission can be due to local variation in the demography or the behaviour of the host such as local aggregations in particular habitats (Mollison 1987). The net result of this is that R_0 will be higher than estimated if it were assumed the population were mixing at random. In this way Mollison & Kuulasmaa (1985) described the way rabies could be maintained in foxes by small mobile foci of higher transmission rates.

When diseases become established they tend to spread as a travelling wave with the velocity strongly dependent on R_0, β, and the length of time the infectious period (Mollison 1987). The rate at which individual diseases spread can vary enormously from 25 km year^{-1} for rabies in red foxes in Europe (Mollison & Kuulasma 1985) to 1000 km year^{-1} for rinderpest in east African ungulates (Plowright 1982).

FMD is endemic in much of the world being absent only from Australia, North America, Central America, New Zealand, Japan, Ireland, Norway and Iceland (Callis 1984). Australia is believed to have had one outbreak of FMD in 1873 (Meischke & Geering 1983). FMD appears to have originated in Africa and be endemic in African buffalo *Syncerus caffer* (Plowright 1988). Buffalo act as carriers for the disease and rarely show any symptoms of acute infection indeed it is suspected that only a few acutely infected individuals are capable of spreading the disease amongst the buffalo population and to other species (Hedger 1976). FMD is known from wild boar in the Caucasus Mountains of Russia (Sludskii 1956) but it is not known whether the disease is endemic in wild boar or maintained by infection from domestic pigs (Kruglikov *et al.* 1985).

The following description of the etiology, symptoms and transmission of FMD comes from Callis (1984). FMD is an acute, highly infectious disease generally of artiodactyls, characterised by the appearance of vesicles on the mouth, nares, muzzle, teats, udder and in ruminants the rumen pillar. The FMD virus is an enterovirus in the picnorvirus group, in the genus aphthovirus and consists of a positive stranded RNA genome of about 8000 nucleotides. There are seven immunological types of the virus with about 60 subtypes.

The first symptoms of FMD are fever, loss of appetite, and salivation followed by the appearance of vesicles up to three cm. in diameter containing clear yellow fluid, in the epithelium of the mouth and feet, particularly the coronary bands. As the vesicles enlarge and erode, the epithelium may slough leaving open wounds that become secondarily infected with bacteria which may cause hoof loss. Mortality from FMD is relatively low in adults 5% with most animals recovering in two weeks, but mortality can be up to 50% in young animals. Death is caused by myocardial lesions which appear as grey streaks in the heart muscle giving the characteristic "tiger heart" of FMD.

The symptoms of FMD can readily be confused with several other vesicular diseases such as vesicular somatitis, vesicular exanthema of swine, and swine vesicular disease. Pigs are susceptible to all of these diseases.

FMD can be spread by direct contact between animals but is dispersed mainly through respiratory aerosols (Pech & Hone 1988). Pigs can excrete up to 30 times more virus particles than other animals and so tend to magnify the disease (Sellers 1971). Wind can play an important role in dispersing the virus over substantial conditions if temperature is low and humidity high (> 70%) (Sellers *et al.* 1977).

The virus is present in most body tissues and will persist for up to 48 hours after death of the host. In muscle tissue inactivation is due to increased concentration of lactic acid. The virus may persist for much longer in bone marrow, lymph nodes and large blood clots, which are buffered against decreasing pH. This opens the possibility of the disease being passed to feral pigs through their appetite for carrion.

FMD is readily partitionable into the categories susceptible, latent, infective, and immune and has been modelled in feral pigs by Pech and Hone (1988) and Pech and McIlroy (1990).

1.5 Thesis Aims

In Giles (1980) study of feral pigs in western New South Wales he suggested that the availability of shelter from the sun and distribution of food were important determinants of where pigs lived. He also lamented the lack of data he was able to collect on movement and ranging behaviour in feral pigs because of poor quality telemetry equipment. The first aim of this study is to redress this shortcoming with an intensive radio telemetry study to derive data on the spatial behaviour of feral pigs. This data is then used to test the hypothesis that seasonal variation in temperature and the distribution of food influences the space use (habitat selection, home-range size, distance moved) of feral pigs. The hypothesis that movements by boars can be influenced by the presence of sows in oestrus is also tested experimentally.

The second aim of this study follows from the recommendations of Pech and Hone (1988) who identified major gaps in our knowledge of feral pig ecology relevant to deriving realistic disease models in feral pigs. Two of these gaps were; knowledge of the population dynamics of feral pigs and contact rates between pigs. This study seeks to build a more realistic model of FMD in feral pigs using data collected in this study on contact rate between pigs and movement rate of pigs and from a concurrent study in the same area on population dynamics. Finally I try to link the parameters important to disease models with the variables purportedly responsible for patterns in the spatial ecology of pigs.

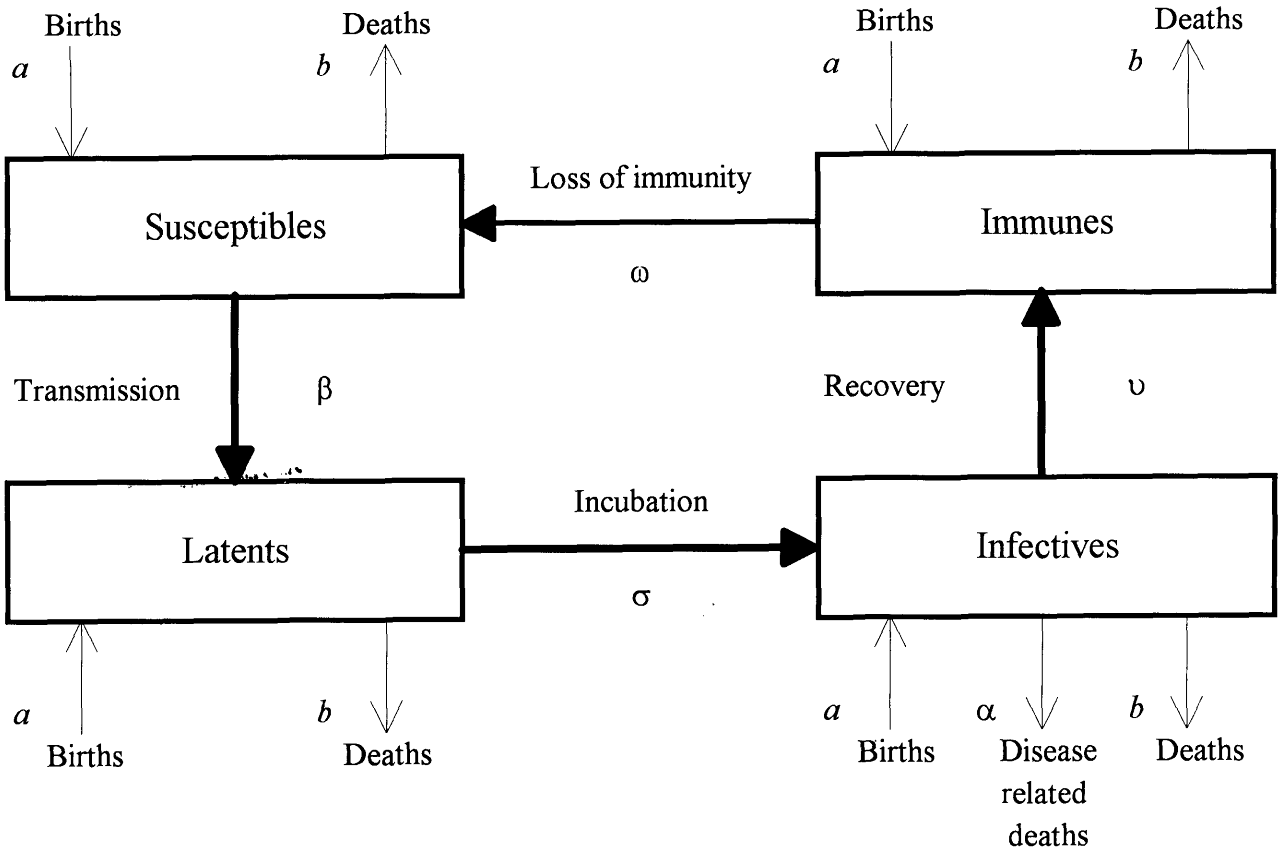


Figure 1.1 Compartmental model of disease epidemic. Parameters described in text.

Chapter 2

The Influence of Temperature and Pasture Biomass on Ecological Parameters of Feral Pigs.

2.1 Introduction

Optimal foraging theory suggests that an animal's preference for a particular habitat will in part reflect the abundance and attractiveness of food in that habitat (Schoener 1987). The limitations of this simplistic model are recognised and a range of constraints have been identified (Stephens & Krebs 1986). Constraints include habitat-specific risk of predation (Price 1984, Lima 1985, Lima *et al* 1985), intraspecific competition for prime habitat (Morris 1989), and the need to return to a central place to consume prey (Orians & Pearson 1979) or fulfil any other self maintaining activity (Jarman pers comm.). Analogous to these constraints is the risk of exposure to lethal temperatures while foraging away from thermal refuges and the different degree of protection from thermal stress, offered by different habitats.

The main determinants of habitat selection by feral pigs and wild boar that have been suggested are (1) dispersion of food (Kurz & Marchinton 1972, Mauget 1981, Baber & Coblentz 1986) and (2) shelter from high temperature (van Vuren 1984, Baber & Coblentz 1986). However, in these studies the effects of food dispersion and temperature on habitat selection were surmised rather than measured.

Throughout much of inland Australia, daily air temperatures frequently rise above 40°C in the shade during summer while the radiant heat load can be much higher. Lacking sweat glands or other physiological means of efficient cooling other than panting (Morrison *et al.* 1967), pigs are very sensitive to high temperatures. Domestic pigs die if exposed to ambient temperatures greater than 38°C (Mount 1968). High temperature has several physiological effects that could influence feral pig behaviour. Increasing ambient temperature suppresses secretion of thyroid hormone which raises body temperature and respiration (Mount 1968). Increasing ambient temperature also reduces appetite and paradoxically, thirst of domestic pigs (Heitman & Hughes 1949). High temperature can be thought of as a potential constraint on where and how far pigs can forage.

The semi-arid rangelands currently represent around 70% of the range that feral pigs inhabit in Australia (Wilson *et al.* 1992). The semi-arid rangelands supports patches of high densities of feral pigs (Giles 1980) and is also where feral pigs come into most conflict with farmers through predation on lambs (Pavlov *et al.* 1981). In semi-arid Australian rangelands there is high variation in both spatial and temporal habitat quality for herbivores (Johnson & Bayliss 1980, Caughley 1987). Temporal variation in habitat quality is due to the dependence of plant growth particularly annual pastures, on sparse unpredictable rainfall (Noy-meir 1973, Robertson 1987). Spatial variation in habitat quality is due mainly to edaphic features of the landscape that vary in fertility and hydrology with low lying areas, particularly drainage basins, having highest moisture levels and fertility (Stafford-Smith & Morton 1990). Pigs in semi-arid rangelands have a flexible diet that can include both carrion and live animals, but consists principally of vegetation (Giles 1980, Pavlov 1980, Littlejohn 1991). The dynamics of feral pig populations in the rangelands are controlled by rainfall driven changes in pasture availability (Giles 1980, Choquenot 1994).

The two most extensive habitats occupied by feral pigs in semi-arid Australia are sand-plains and flood-plains. Sand-plains consist of aeolian red sands and red earths usually covered with sparse shrubby vegetation. Flood plains are associated with rivers, consist of grey cracking clays and support a variety of vegetation types. Pastures in these two habitat types respond differently to rainfall; germinating earlier on the sandplains but dying off earlier after rainfall, on the floodplains (Wellard 1987). Choquenot (1994) demonstrated that rate of decrease of feral pigs, during drought, was lower in sites with higher proportions of flood plain than sites with higher proportions of sand plains.

The most intensive study of feral pigs in the semi-arid rangelands was by Giles (1980) at Yantabulla, north-west New South Wales. His study demonstrated the strong dependence of feral pig population growth rate and body condition on pasture biomass. He also suggested habitat preference for pigs was governed by a combination of the availability of dense shelter, water and food. Choquenot (1994) extended Giles work to derive population models for feral pigs based on data from a number of sites along the Paroo River including Nocoleche Nature Reserve where the current study was conducted.

In wild pigs a range of interconnected behavioural and physiological parameters such as home-range size, distance moved and nutritional status are responsive to temporal and spatial variation in food supply (Oloff 1950, Barret 1978, Giles 1980, Baber & Coblentz 1986, Baber & Coblentz 1987). In particular home-range size is known to increase with decreasing food supply (Singer *et al.* 1981). The bioenergetic explanation is that pigs have to search further to satisfy their hunger. However home-range may also be influenced by constraining environmental variables such as very high temperature, when exposure to the sun may limit the distance pigs can travel away from cover and water. This chapter seeks to find out how behaviourally flexible feral pigs are by examining the changes in three linked behavioural parameters; (1) habitat preference, (2) home-range size and (3) hourly distance moved and a single physiological parameter, adult body weight, (in order to index change in nutritional stress). These parameters are compared with the changing distribution and abundance of food during and after a drought and variation in a potentially constraining ecological factor, high temperature.

The practical consequences of the results of this chapter for modelling FMD dynamics include the potential effect of environmental variables such as dispersion of food amongst different habitats and temperature on behavioural characteristics such as habitat selection and movement, and the influence of behavioural changes on the dynamics of an FMD epizootic. Strong habitat preference may enhance spatial aggregation which may elevate the contact rate between individual pigs, influencing the probability of disease establishment and persistence (Anderson & May 1991). Similarly, the velocity of the advance of an epizootic will be strongly influenced by the movement rate of the host (Mollison 1987, Pech & McIlroy 1990). Therefore the parameters measured and analysed in this chapter have application beyond the interpretation of the behaviour and ecology of feral pigs at Nocoleche. They will be converted to parameters useful for disease modelling and entered into a full FMD model in Chapter 4.

2.2 Study Area

The study was conducted in Nocoleche Nature Reserve north-western New South Wales, Australia 144° 8' E, 29° 50' S (Figure 2.1). Rainfall is sparse and erratic, averaging 193 mm with a 100 year standard deviation of 94 mm (Australian Bureau of Meteorology Records) (Figure 2.2). Summers are hot and long while winters are brief and mild (Figure 2.3). The topography is flat and the hydrology dominated by the Paroo River and Cuttaburra Creek, which form a series of interconnected channels and anabranches that flow only occasionally during flood. Vegetation type in Nocoleche is strongly associated with soil type (James 1960, Bayliss 1978). The four main habitats determined by soil and vegetation comprise:

1) Shrubland: This habitat was dominated by the shrubs hop bush *Dodonea attenuata*, and turpentine *Eremophila sturtii*, on soft red sands of aeolian origin. There are occasional emergent white wood *Atalaya hemiglauca*, and leopard wood *Flindersia maculosa* trees. Ground cover consisted of annual species of grasses *Aristida* spp. and annual chenopod forbs *Bassia* spp., and *Atriplex* spp. This was the

most extensive habitat in the Reserve and was furthest from the Paroo River occupying most of the western side of the study site.

2) Riverine woodland: This habitat was confined to black cracking, self mulching clay soils along the Paroo River and its anabranches. The dominant plant species in this community was the generally leafless shrub lignum *Muehlenbeckia florulenta* which occurred in dense tangled thickets up to several ha in extent. There was an extensive tree over storey of coolibah *Eucalyptus microtheca*, river red gum *Eucalyptus camaldulensis*, yapunyah *Eucalyptus ochrophloia,* and cooba *Acacia stenophylla.* The under storey was dominated by tussocks of the perennial grass *Paspalidium jubiflorum.* Less common components of the understory included annual grasses *Aristida* spp. and annual forbs such as *Solanum esuriale*, *Centipeda cunninghamia* and *Teucrium racemosum.*

3) Woodland: This habitat was associated with hard compact mottled red-grey clays that are subject to water logging. This habitat is usually between the riverine woodland and the shrubland and dominates the eastern part of the study site. Woodlands are dominated by sparse lignum which occurs as individual plants rather than dense thickets as in the riverine woodland, and scattered yapunyah and cooba. The under storey was similar in composition to the riverine woodland but much sparser. The most noticeable feature of this habitat were extensive areas of bare ground up to several km^2 in size.

4) Ephemeral swamps: These were irregularly inundated areas of red-grey or black clay soil. They may be ancient creek meanders, or terminal basins for small fluvial systems. They were usually entirely contained within shrublands and may be several ha to several km^2 in extent. Ephemeral swamps are bounded by bands of trees such as black box *Eucalyptus largiflorens* and bimble box *Eucalyptus populnea.* Pasture on the swamps varied considerably but included annual grasses *Aristida* spp. and *Enteropogon* spp., and annual forbs such as *Centipeda cunninghamia*, *Portulaca interranea*, and *Mimulus repens.*

The distribution of habitat types is shown in Figure 2.4. The woodland and riverine woodland correspond to floodplain habitat while the shrubland corresponds to sandplain habitat of other studies (Johnson & Bayliss 1981, Priddel 1987). All habitats except ephemeral swamps had permanent water as either a river channels in woodland and riverine woodland or earth tanks in shrubland. In declining order of water availability riverine woodland had the most, followed by woodland, shrubland and then ephemeral swamps. In Chapter 1 it was noted that pigs tend to have wallows within their home-ranges. In this study pig wallows were noted in all habitats at all water sources.

Dingoes *Canis familiaris*, the only significant non-human predator of feral pigs are absent from the Nature Reserve and are extensively controlled throughout north-west New South Wales. Feral pigs are controlled throughout Nocoleche Nature Reserve by trapping and helicopter shooting. Other large herbivores besides feral pigs, common in the Reserve besides feral pigs, were red kangaroos *Macropus rufus*, eastern grey kangaroos *Macropus giganteus*, feral goats *Capra hircus*, and emus *Dromaius novaehollandiae*.

2.3 Methods

RADIO TELEMETRY

Pigs were trapped in steel mesh traps baited with soaked wheat (Choquenot *et al.* 1993). Once caught they were subdued with a combination of xylazine hydrochloride and ketamine hydrochloride. Body weight, head length, head body length and hind foot length were recorded as was age based on tooth eruption pattern (Matschke 1967). All pigs captured received a unique pattern of four coloured plastic button ear tags. A subsample of 38 adult pigs were fitted with radio collars (Titley Electronics) over an 18-month period prior to and during the study.

Seven radio tracking sessions were conducted at approximately three month intervals between November 1991 and July 1993. Each tracking session consisted of between five and 10 days monitoring of the position of all pigs at hourly intervals from three 12m radio telemetry masts (four masts in July 1992). Each mast was fitted with two seven element yagis (Biotelemetry, Australia). Masts were usually positioned approximately 3.5 km apart but the actual positions varied according to access during flooding and the dispersion of the pigs. During tracking, the tracker at each station would scan for a set sequence of pigs at the beginning of each hour, on a Telonics TR-4 Receiver. When a signal was received the tracker recorded to the nearest degree the bearing where the signal strength was greatest. This procedure was repeated at the beginning of each subsequent hour. Trackers kept in radio contact to synchronise the taking of bearings. Individual trackers varied between sessions but each was given a brief training session before commencing tracking. The overall accuracy of bearings was tested by reference to hidden transmitters. These transmitters were not identified as reference transmitters to the trackers and were included in the sequence of transmitters on pigs to be tracked.

The number of pigs tracked varied between tracking sessions from seven to 22. This was due partly to equipment failure and death of the collared pigs but mainly to animals moving in and out of the study area. Tagged pigs moved up to 50 km from their point of capture over the two years of this study. During each tracking session there were females of all reproductive states (pregnant, non-pregnant, and non-pregnant lactating).

Telemetry error was calculated using the maximum likelihood estimator available in LOCATE II (Nams 1990). This gives an estimate of the standard deviation of the bearing angles for each location estimated using more than two bearings. The mean standard deviation for a random sample of 146 locations covering all pigs and all tracking sessions was 5.4°.

PASTURE BIOMASS

To index food supply, pasture biomass in each habitat type was measured prior to each tracking session using the comparative yield technique (Haydock and Shaw 1975). This technique estimates pasture biomass in a $0.25m^2$ quadrat against a sequence of photographs of quadrats of known pasture biomass. There were nine photographic standards covering a range of pasture types varying in height, density and species composition, made up during the course of the study. To assess habitat specific pasture biomass more than 30 quadrats in each of the four habitats were assessed by myself against photographic standards of known biomass prior to each tracking session. Biomass was not assessed in the woodland in July 1992 and is therefore interpolated from the April 92 and October 92 results.

TEMPERATURE

To index thermal stress, daily maximum temperatures for the duration of each tracking session were collected from a New South Wales National Parks and Wildlife Service weather station within the study area. It is recognised that mean maximum temperature is only an index of heat stress. It is likely that pigs could be exposed to much higher radiant heat loads in summer if they venture from cover. However, mean maximum temperatures here indicate relative differences between seasons in potential heat stress.

COVER

To index which habitats on average gave pigs most protection from high temperatures, cover was estimated in 150, 20m x 20m randomly located quadrats covering all four habitats using the Daubenmire Cover Scale (Daubenmire 1959). To use this scale an observer ranks the percentage of area covered by a particular vegetation type from a scale of 1 (0% - 5%) to 6 (95% - 100%). Cover estimates were taken for three vegetation strata: Upper tree layer (> 8m), lower tree layer

(3m - 8m), and shrub layer (0.5m - 3m) and expressed as a mean cover percentage. Unlike temperature and pasture, cover was only estimated once because cover is reckoned to be a static quality over the time period of the study despite some leaf fall from the upper canopy during drought.

There were qualitative differences in the type of cover in the lowest strata between habitats. In the riverine woodlands and to a much lesser extent the open woodlands the cover was dominated by dense thickets of lignum up to 2m high, often with runways constructed by the pigs under the dense low canopy. In the ephemeral swamps the lowest cover tended to be low (<1m) clumps of spiny lignum *Muehlenbeckia horrida* that were usually concentrated around the periphery of the swamps. Low cover was more evenly dispersed in the shrublands than other habitats chiefly as upright sparse hop bush or turpentine shrubs. Occasional clumps of dense cover of saltbush *Enchylaena* spp. occurred under the few trees in this habitat and this was usually where resting pigs or their bedding sights were seen rather than beneath the abundant hop bush or turpentine.

HABITAT USE

To map the broad scale distribution of habitat types a geometrically corrected SPOT satellite image of the area was used. This image was classified and the classification ground-truthed and corrected to give the four broad habitat types (Butson 1992). More fine grained definition of habitat was possible but because of the error associated with radio telemetry (Nams 1989), the analysis was restricted to the four coarse habitat classifications described.

The limits of the study area were defined by a minimum convex polygon of the outer most locations for any pigs during the entire study period. This polygon defined the area that pigs were assumed to have available for foraging at some time (Porter & Church 1987). This polygon was approximately 104 km^2. The proportions of the four habitat types in this study area polygon were 30.2% woodland, 15.1% riverine woodland, 51.4% shrubland and 3.3% ephemeral swamps.

To determine habitat use all telemetred locations of pigs deemed valid were overlaid on to the SPOT habitat image and the habitat at each location recorded. The number of locations in each of the four habitats for each pig during a tracking session were expressed as proportions of the total number of locations for that pig in that tracking session. As the sum of these proportions for each pig equals one they represent a composition and hence cannot be considered independent of one another. As such they must first be converted to log-ratios prior to analysis (Aitchison 1986). To convert the proportions of habitat used by each animal in each tracking session, to log-ratios, proportions of habitat use, for each tracking session, for three of the habitats (U_1, U_2, U_3) were divided by the proportion of habitat use by that animal for the fourth habitat U_4 and converted to natural logarithms (Aebischer *et al.* 1993). This gives three log-ratios; $Y_1 = \ln(U_1/U_4)$, $Y_2 = \ln(U_2/U_4)$, $Y_3 = \ln(U_3/U_4)$ from four proportions of habitat use for each pig in each tracking session. In this case the proportional use of woodland was used as the denominator, although any of the four habitats could have been used. If a habitat was not utilised by an individual pig, 0.001 was entered as the proportional use of that habitat, an order of magnitude smaller than the lowest proportional use by any pig of any habitat. This technique has the advantage of avoiding the lack of independence in intensively sampled radio telemetry data without sacrificing biologically useful information.

The two main questions asked about habitat preference were (1) how habitat preference changes over time, and (2) what environmental variables caused these changes. Before assessing these questions it had to be established that habitat selection does in fact change over time, and to determine whether habitat selection differs between boars and sows. To answer these questions, the three log-ratios of habitat use for all pigs use were entered as dependent variables in a two-way

MANOVA with tracking sessions (1-7) and sex (male/female) as categories, with significance assessed using the multivariate Wilk's Λ criterion available for MANOVA in SAS (SAS Institute 1988). There were significant differences between tracking sessions in habitat use (Wilk's $\Lambda = 0.578$, $P<0.0006$) so a more detailed investigation of how change occurred was justified. However, there was no significant difference in habitat use between males and females (Wilk's $\Lambda = 0.991$, $P<0.869$) or in the interactive term (Wilk's $\Lambda = 0.759$, $P<0.111$) consequently habitat use for both sexes were pooled for subsequent analyses.

To determine which habitats were preferred in which tracking sessions, a habitat preference ranking for the four habitats for each session was calculated using the compositional analysis technique described by Aebischer *et al.* (1993). The preference ranking is calculated by constructing a four by four matrix of the difference between habitat use and habitat availability for each pig at each tracking session. Each column and row in this matrix corresponds to one of the four habitat types. Each element within the matrix consists of the difference between the log-ratio of row over column habitats utilised, and the log-ratio of row over column habitat available. Utilisation was estimated by the proportion of locations within a habitat, while availability was estimated by the proportion of habitat within the convex polygon described by the outermost locations for all pigs over all trips as this polygon is the total area pigs are assumed to have available for foraging at some time. Each element can be represented by

$$a_{ij} = \ln(U_i/U_j)-\ln(A_i/A_j) \qquad (2.1)$$

where a_{ij} is the ijth element, U_i is utilisation in habitat i, U_j is utilisation in habitat j, A_i availability of habitat i, A_j is availability of habitat j.

The hypothesis that one habitat is preferred to another is tested by first summing the log-ratio differences a_{ij}, for all pigs for each trip. From this the mean and standard error for each log-ratio difference for each session is calculated and the ratio of the standard error to mean gives the *t*-ratio. This can be checked for significance using a table of *t* distributions (Aebischer *et al.* 1993).

To represent the preferences for one habitat over another calculated previously, another 4 by 4 matrix of habitat types is constructed. For each element, a positive *t*-ratio indicates that the habitat in the row is preferred over the habitat in the column and it is given a positive sign (+). A negative *t*-ratio indicates that habitat in the column is preferred over the habitat in the row and a negative sign is given (-). If the preference is significant at the $P<0.05$ level triple signs are given (+ + +) for positive and (- - -) for negative. The preference rank for each habitat is then established by summing the number of positive signs in a habitat row in the *t*-ratio matrix. The habitat row with completely positive signs is the most preferred.

To determine whether pasture biomass and temperature influenced habitat utilisation, these variables were analysed by stepwise multivariate regression. In this model the three log-ratios of habitat use described earlier, are symbolised by Y_1 = ln(riverine woodland/woodland), Y_2 = ln(shrubland/woodland) and Y_3 = ln(swamp/woodland), were considered the three dependent variables. The independent variables were the natural logarithm (to normalise the data) of mean pasture biomass kg ha^{-1} for each of the four habitat types (F_1 = woodland, F_2 = riverine woodland, F_3 = shrubland, F_4 = ephemeral swamps) and the mean maximum temperature = T. Hence, the model for the multivariate regression was

$$Y_1,Y_2,Y_3 = \alpha+\beta_1F_1+\beta_2F_2+\beta_3F_3+\beta_4F_4+\beta_5T \quad (2.2)$$

The hypothesis that the regression parameters for each of the independent variables were the same for all dependent variables is tested using the Wilk's Λ criterion available through MTEST in SAS (SAS Institute 1988). A significant result for any independent variable indicates that variable explains a significant proportion of the variance for the composition of habitat utilisation.

To investigate how use of individual habitats are influenced by pasture biomass and temperature it is easiest to first create the four log-ratios of $Z_1=\ln[U_1/(U_2+U_3+U_4)]$, $Z_2=\ln[U_2/(U_1+U_3+U_4)]$, $Z_3=\ln[U_3/(U_1+U_2+U_4)]$, and $Z_4=\ln[U_4/(U_1+U_2+U_3)]$. Z_1,Z_2,Z_3, and Z_4 are the ratios of use of one particular habitat to the use of other habitats combined recalling that U_1 is utilisation of woodland, U_2 is utilisation of riverine woodland, U_3 is utilisation of shrubland, U_4 is utilisation of ephemeral swamps. Therefore to determine how use of individual habitats is influenced by pasture biomass and temperature, Z_1,Z_2,Z_3, and Z_4 are individually regressed using stepwise multiple regression, on the independent variables F_1,F_2,F_3,F_4 and T (Aebischer pers. comm.). Examining the sign of the regression coefficients will indicate how the numerator utilisation changes in proportion to utilisation of the rest of the habitats.

To assess how habitat use changed throughout the day the proportion of locations in each habitat in each hour (0 - 2300) for all the collared pigs, were combined for all days in each tracking session. While change in preference can be neither inferred from this data nor analysed because it is serially auto-correlated, it indicates daily trends in habitat use.

In summary there will be three results of the analysis of habitat preference and use; (1) a preference ranking for each habitat during each tracking session, (2) the influence of environmental parameters on changes in habitat use, and (3) the daily changes in habitat use.

HOME-RANGE SIZE

Home-range size was estimated by the minimum convex polygon method for each tracking session over a standard time of five days. The minimum convex polygon method was chosen over more sophisticated statistical techniques because all that is required for the analysis presented here is an index rather than an absolute estimate of home-range size. The minimum convex polygon also does not have the restrictive requirement that the data be independent. Before analysing the effects of pasture biomass and temperature, differences in home-range size between tracking sessions and between sexes were compared by ANOVA. There was a significant difference in home-range size between sexes ($F_{1,78}=11.06$, $P<0.0026$) but no significant differences between tracking sessions ($F_{6,78}=1.04$, $P<0.807$) or any interactive effect ($F_{6,78}=1.04$, $P<0.807$). When analysed separately male home-range did not change significantly over time ($F_{5,37}=0.31$, $P<0.90$) while female home-range did ($F_{6,46}=4.33$, $P<0.048$). Therefore female home-range size was entered as the dependent variable in a stepwise multiple regression. The same independent variables used in the analysis of habitat selection were entered; ln mean kg ha^{-1} of pasture biomass in woodland, riverine woodland, shrubland, ephemeral swamps, and mean maximum temperature.

MOVEMENTS

Hourly movements were measured by calculating the distance between successive locations separated by one hour for each pig in each tracking session. These hourly differences were averaged for each pig in each tracking session. To determine whether data for the sexes should be pooled the hourly distances moved by boars and sows were entered as the dependent variable in a two-way ANOVA, with tracking session (1-7) and sex as factors. The results showed that there were significant differences between tracking sessions ($F_{6,78}=4.44$, $P<0.006$), the differences between sexes were only just non-significant at the $P<0.05$ level ($F_{1,78}=0.31$,

$P<0.059$), while the interaction between tracking session and sex was non-significant ($F_{1,78}=0.731$, $P<0.731$). As with the analysis of home-range mean ln kg ha^{-1} of pasture biomass in woodland, riverine woodland, shrubland, ephemeral swamps, and mean maximum temperature were entered as independent variables with mean hourly distance moved for both sexes combined as the dependent variable in a step-wise multiple regression.

To determine how hourly distance moved changed during the course of the day the average distance moved in each hour (0-2300) by all pigs was calculated for each tracking session. As with daily variation in habitat use these data are serially auto-correlated and hence were used to indicate daily trends in activity only.

LIVE WEIGHT

The live weights of all pigs over one year old, as indicated by the eruption of the second molar (Matschke 1966), were used in this analysis. As with the analysis of habitat preference, home-range size, and distance moved, the data on live weights were tested for significant differences between the sexes and tracking sessions with a two way ANOVA before determining the effect of pasture biomass and temperature on live body weight. There was a significant effect of tracking session ($F_{6,97}=4.62$, $P<0.0004$), but sex was not significant ($F_{1,97}=3.39$, $P<0.0685$), nor was the interaction between sex and tracking session significant ($F_{1,97}=1.29$, $P<0.268$). Unlike habitat utilisation, home-range size, and distance moved, which can in theory respond instantaneously to changes in environmental conditions live weight will be the cumulative result of a number of variables that have been operating in the recent past. While it is valid to consider the effect of mean pasture biomass measured at the same time the pigs were weighed (current pasture biomass being in part the result of past pasture biomass), mean maximum temperature has no such "memory". Hence, for this analysis mean maximum temperature for the month preceding the first day traps were set for pigs was used, instead of the mean maximum temperature during the tracking session. Therefore mean ln kg ha^{-1} of pasture biomass in woodland, riverine woodland, shrubland, ephemeral swamps, and mean maximum temperature for the preceding month were entered as independent variables with live body weight for both sexes as the dependent variable in a step-wise multiple regression.

2.5 Results

PASTURE BIOMASS

The overall change in pasture biomass reflected a shift from sparse vegetation during late 1991, early 1992 during an El Niño induced drought to abundant vegetation following heavy rains in late 1992 although the change is not consistent between habitats (Figure 2.5). A summary of the growing conditions during the course of this study as indexed by monthly rainfall, is shown in Figure 2.6.

TEMPERATURE

The mean maximum temperatures are shown in Table 2.1. The highest individual temperature during a tracking session was 40° C in November 1991. The temperatures preceding trapping sessions were substantially different to temperatures during tracking in winter and spring because these are transitional times for temperature change, temperature increasing during spring and decreasing during autumn.

Table 2.1 Mean maximum temperature in C° ±1SE

Tracking Session	Mean Maximum Temperature During Tracking Session C° ±1SE	Mean Maximum Temperature for Month Preceding Trapping C° ±1SE
November 91	35.9 ±2.1	31.7±0.9
February 92	34.6 ±1.7	36.4±1.0
April/May 92	24.2 ±0.6	31.8±0.6
July 92	16.2 ±0.7	18.2±0.4
November 92	32.9 ±1.7	28.2±0.9
April 93	26.5 ±1.1	30.3±0.7
July 93	17.5 ±0.8	17.7±0.6

COVER

The mean cover percentage of the three vegetation strata within each habitat are shown in Table 2.2. The interpretation of these data is that riverine woodland offered pigs the most protection from direct sun, with woodland next, offering intermediate protection, followed by shrubland and ephemeral swamps offering the least protection. This means that while an individual pig can find all of its cover requirements in any habitat it will on average find sufficient cover more frequently in riverine woodland.

Table 2.2 Mean Daubenmire percentage cover for four vegetation strata in each habitat.

	Upper tree layer	Lower tree layer	Shrub layer	*n*
Riverine woodland	27.2	2.7	31.5	36
Open woodland	9.7	2.1	17.6	37
Shrubland	2.2	1.1	24.7	53
Ephemeral swamps	13.7	0.4	6.0	20

HABITAT PREFERENCE

The distribution of the 8,218 locations obtained are shown in Figures 2.7 to 2.13. The mean percentages of locations in each of the four habitats are displayed in Fig. 2.14. The trend is for use of riverine woodland to decrease over time and for use of shrubland and ephemeral swamps to increase.

There were significant habitat preferences in all tracking sessions and preference rank changed between tracking sessions (Table 2.3). The riverine habitat was the most preferred habitat except in July 1992 and 1993 when shrubland was most preferred. Woodland and ephemeral swamps alternated as the least preferred with ephemeral swamps tending to be more preferred during winter.

The switch in preference during July (the southern winter) is suggestive that temperature plays a part in habitat selection. This is confirmed in the results of the multivariate test which for the model:

$$Y_1, Y_2, Y_3 = \alpha + \beta_1 F_3 + \beta_2 T \qquad (2.3)$$

gives a significant result of (Wilk's $\Lambda=0.898$, $F_{3,87,}=3.276$, $P<0.0248$). This indicates both pasture biomass in shrubland and temperature are important determinants of the composition and hence overall habitat selection.

The results of the regressions of Z_1,Z_2,Z_3, and Z_4 on pasture biomass in the four habitats and mean maximum temperature can be seen in Table. 2.4. The interpretation of these results is straightforward. For Z_1, utilisation of woodland increases with decreasing pasture biomass in shrubland; for Z_2, utilisation of riverine woodland increases with decreasing pasture biomass in shrubland and increasing temperature; for Z_3, utilisation of shrubland increases with increasing pasture biomass in shrubland and decreasing temperature; for Z_4, utilisation of ephemeral swamps increases with decreasing temperature.

November 91 (n+14)

	Woodland	Riverine	Shrubland	Swamp	Rank
Woodland		- - -	+	+ + +	2
Riverine	+ + +		+ + +	+ + +	3
Shrubland	-	- - -		+ + +	1
Swamp	- - -	- - -	- - -		0

February 92 (n=7)

	Woodland	Riverine	Shrubland	Swamp	Rank
Woodland		-	-	+	1
Riverine	+		+ + +	+ + +	3
Shrubland	+	- - -		+	2
Swamp	-	- - -	-		0

April/May 92 (n=14)

	Woodland	Riverine	Shrubland	Swamp	Rank
Woodland		- - -	-	-	0
Riverine	+ + +		+	+	3
Shrubland	+	-		+	2
Swamp	+	-	-		1

July 92 (n=22)

	Woodland	Riverine	Shrubland	Swamp	Rank
Woodland		- - -	- - -	-	0
Riverine	+ + +		-	+	2
Shrubland	+ + +	+		+	3
Swamp	+	-	-		1

November 92 (n=17)

	Woodland	Riverine	Shrubland	Swamp	Rank
Woodland		-	-	+	1
Riverine	+		+	+	3
Shrubland	+	-		+ + +	2
Swamp	-	-	- - -		0

April 93 (n=8)

	Woodland	Riverine	Shrubland	Swamp	Rank
Woodland		- - -	-	+	1
Riverine	+ + +		+	+	3
Shrubland	+	-		+	2
Swamp	-	-	-		0

July 93 (n=10)

	Woodland	Riverine	Shrubland	Swamp	Rank
Woodland		-	- - -	-	0
Riverine	+		- - -	-	1
Shrubland	+ + +	+ + +		+	3
Swamp	+	+	-		2

Table 2.3 Ranking matrices of log-ratio differences between utilized and available habitat for all tracking sessions, + indicates habitat in row preferred to habitat in column, - indicates habitat in column preferred to habitat in row. Triple sign indicates preference significant at $P<0.05$.

Table 2.4 Regression equations of the four log-ratios of $Z_1=\ln[U_1/(U_2+U_3+U_4)]$, $Z_2=\ln[U_2/(U_1+U_3+U_4)]$, $Z_3=\ln[U_3/(U_1+U_2+U_4)]$, and $Z_4=\ln[U_4/(U_1+U_2+U_3)]$ on food abundance in shrubland ln kg ha^{-1} (F_3), and mean maximum temperature C^{o} (T).

Regression Equation	R^2	F	Significance
Z_1 = -1.81-0.007F_3	0.06	5.55	$P<0.021$
Z_2 = -2.48-0.01F_3+0.045T	0.195	21.8	$P<0.0001$
Z_3 = 0.762+0.006F_3-0.046T	0.2	11.08	$P<0.0001$
Z_4 = -1.44-0.14T	0.11	11.39	$P<0.0011$

The daily variation in habitat use can be seen in Figure 2.15. From this it can be seen that use of riverine woodland increased during the afternoon in November 91, and February 92 perhaps due to a requirement to seek shelter in the thick cover of riverine woodland, or drink and wallow in the water most abundantly available in riverine woodland. However, this trend was not observed during the other hot tracking session in November 92, when most use of riverine woodland was made during the hours of darkness from 2200 hours to 500 hours. The overall trend is one of little daily variation in habitat use.

HOME-RANGE SIZE

The regression of pasture biomass and temperature on female home-range size was significant (Table 2.5). Female home-range size increased with decreasing food abundance in shrubland, decreasing temperature, and increasing abundance of food in swamps. This effect was only noticeable in April and July 1992. The lack of change in home-range size in males and the difference in home-range size between the sexes can be seen in Figure 2.16. Female home-range size only approached male home-range size during April 92 and July 92 coinciding with sparse pasture biomass and cool conditions.

Table 2.5 Regression equation of female home-range size in km^2 (Y), on food abundance in shrubland ln kg ha^{-1} (F_3), food abundance in ephemeral swamps ln kg ha^{-1} (F_4), and mean maximum temperature C° (T).

Regression Equation	R^2	F	Significance
$Y = 11.61 - 1.35F_3 + 0.845F_4 - 0.20T$	0.23	2.32	$P<0.048$

MOVEMENTS

The regression of pasture biomass and temperature on hourly distances moved was significant (Table 2.6). Distances moved decreased with increasing pasture biomass in shrubland. The change in distance moved tends to mirror the changes in female home-range size, although distance moved declines markedly after April 92 unlike female home-range size (Figure 2.17).

Table 2.6 Regression equation of hourly distance moved in m (*Y*), on food abundance in shrubland ln kg ha^{-1} (F_3).

Regression Equation	R^2	F	Significance
$Y = 715.7 - 45.63F_3$	0.08	8.06	$P<0.0056$

The daily changes in distance moved are shown in Figure 2.18. Distances moved tend to be greatest at night with the difference most pronounced during the warmer months of November and February but less so in November 92. The shortest distances moved tend to coincide with the hottest time of the day, during the mid-afternoon 1400 to 1500. There was a pronounced increase in distances moved immediately after sunset in all seasons. This is probably when pigs are moving from their bedding places to feed and to drink.

LIVE WEIGHT

The result of the regression of pasture biomass and temperature on live weight was significant (Table 2.7). Body weight increased with increasing pasture biomass in woodland and with decreasing temperature. The trend can be seen when comparing changes in body weight (Figure 2.19) with changes in pasture biomass in woodland.

Table 2.7 Regression equation of live body weight (*Y*), on food abundance in shrubland ln kg ha^{-1} (F_1), and mean maximum temperature in the preceding four weeks C° (*T*).

Regression Equation	R^2	F	Significance
$Y = 4.3+11.53F_1-0.262T$	0.24	29.9	$P<0.001$

2.5 Discussion

The general result of this study is that the environmental parameters; pasture biomass in the four habitats and temperature had some influence on the parameters; habitat utilisation, home-range size, distance moved and body weight. The most influential variables were pasture biomass in shrubland which had an influence on overall habitat selection, home-range size, and distance moved while temperature influenced overall habitat use home-range size, and body weight.

Habitat selection in feral pigs is influenced by both pasture biomass in shrubland and mean maximum temperature. This is despite shrubland being the preferred habitat in only two of the seven tracking-sessions. Use of shrubland increased with increasing pasture biomass in shrubland and decreasing temperature to peak in the winter months of July 92, and July 93 when shrubland was the preferred habitat. In this they partially resemble the sympatric native herbivores red kangaroos and grey kangaroos *Macropus fuliginosus* which shift preference from floodplains to sandplains when drought breaks (Priddel 1987). The preference for shrubland in July 92 was despite shrubland having a very much lower pasture biomass than in any other habitat. A possible reason for this may be the dominance of pasture in riverine woodland by the rather coarse grass *P. jubiflorum*, which may have been less palatable than the more tender annual grasses and chenopods that dominated pasture in shrubland. The decline in use of shrubland with increasing temperature is understandable given the relatively little shelter from heat available in this habitat. In a study of the thermal ecology of kangaroos in western New South Wales Dawson and Denny (1969) noted that while only 20% of solar radiation penetrated *Acacia* shrubs that had similar structure and cover to the *D. attenuata* and *E. sturtii* shrubs at Nocoleche, the radiation temperature under these shrubs exceeded the animals body temperature by up to 30°C.

Riverine woodland was preferred habitat in five of seven tracking sessions. These findings agree with Baber & Coblentz (1986) who noted a preference for well watered shady canyon bottoms during summer, with Barrett (1982) who noted a general preference for dense cover, and with Gerard *et al.* (1991) who noted a preference for bedding sites with "natural roofs" during hot weather. Indeed a strong preference for riparian habitat or vegetation associated with permanent water bodies is common to a diverse range of mammals (Jarman 1972, Carson & Peek 1987, Dinerstein & Price 1991, Fischer & Hollen 1991) although whether these animals are selecting these habitats because of increased availability of food, water, or shelter from extreme temperature and predators, is not clear. Riverine woodland offered most protection from heat stress in the dense thickets of lignum around the Paroo River and the most extensive water supply. As stressed in Chapter 1, water is important not only for drinking but providing mud to wallow in to lower body temperature. In an animal house experiment Heitman and Hughes (1949) showed that despite access to drinking water pigs showed signs of severe distress including high body temperature and increased respiration rate at an ambient temperature of 38°C. This was not alleviated by fanning the pigs with dry air. However, if pigs were allowed to wet themselves both respiration rate and body temperature fell. Pigs were often seen wallowing in the mud on the bank of the Paroo river during the hottest weather. A further attraction of the riverine woodland was the availability of lignum roots which Littlejohn (1991) showed to be a highly utilised food by pigs at Nocoleche during the hot dry conditions at the beginning of 1991. This high level of utilisation disappeared by April 1991 when forbs and grasses dominated the diet. It is also possible that lignum roots are a reliably available food supply in a habitat pigs prefer because of its extensive availability of cover and water.

While there was a low overall preference for woodland, it was preferred almost as much as riverine woodland in November 1991. After November 91 woodland was always either the least or second least preferred habitat. Despite floristic similarities with riverine woodland mentioned in the description of the study site, woodland had much less cover and pasture biomass than riverine woodland.

Despite having some of the highest pasture biomass, ephemeral swamps were along with woodland the least preferred habitat. Ephemeral swamps are inundated only occaisionally in contrast to the permanently inundated reed swamps preferred by feral pigs (Giles 1980) and wild boar (Dardaillon 1987). In the Northern Territory, Hone (1990) noted that use of floodplain habitat (similar to the ephemeral swamp habitat in this study) changed dramatically between the wet season when it was inundated and extensively used by feral pigs and the dry season when it was not inundated and little used. Use of ephemeral swamps increased with decreasing temperature, probably because of all habitats, it generally had the least cover and water, offering the least protection from heat stress. Even so they were not highly preferred during the cool months of 1992 despite having relatively high pasture biomass and abundant water. A further factor in the lack of preference for the ephemeral swamps could have been the pasture composition, which was dominated by short dense swards of the highly aromatic sneeze-weed daisy *C. cunninghamia* the scent of which may not have been attractive to pigs although kangaroos were frequently seen grazing these swards during drought. The low growth structure of the sneeze-weed swards may also have made them difficult for pigs to graze.

The larger home-range size of males accords with other studies of wild boar and feral pigs (Kurz & Marchinton 1972, Singer *et al.* 1981, Mauget 1981, Baber & Coblentz 1986, McIlroy 1989, Saunders & Kay 1990, Cayley 1993). This phenomenon is common to some mammals (Jenkins 1981), the postulated reason being that males need to cover the home-ranges of as many females as possible while female home-range size is dictated by the dispersion of food. As such this is an extension of Bateman's hypothesis (Bateman 1948) that male reproductive success is limited by access to females while female reproductive success is limited by access to resources.

Comparison of home-range sizes of pigs at Nocoleche with other studies of feral pigs and wild boar is difficult because each worker tends to sample over a different time scale and at different intensities. One trend though that is obvious is that the average five day home-range size of pigs at Nocoleche is larger than the home-range of size of wild pigs in mesic habitats aggregated over an entire study. The aggregate home-range size for wild pigs in humid North American forests was 3.5 km^2 for males and 3.1 km^2 for females while in a humid New Zealand forest aggregate home-range size was even smaller varying from a maximum of 2.04 km^2 to a minimum 0.28 km^2 (McIlroy 1989). In Australia, Saunders and Kay (1990) measured mean aggregate home-range sizes of 10.9 km^2 for males and 4.7 km^2 for females in temperate highland forests. The largest aggregate home-ranges reported was 31.2 km^2 for boars and 19.4 km^2 for sows in the wet-dry tropics of the Northern Territory (Cayley 1993). The probable reason for the smaller home-range size in more mesic habitats is the likely much higher density of food although none of these studies have measured food availability.

Female home-range size was influenced by the same variables influencing habitat use. In other studies of feral pigs and wild boar, increases in home-range size have been associated with seasons of poor mast crop in Tennessee (Singer *et al.* 1981) and seasonal lows in pasture abundance during winter in the highlands of New South Wales (Saunders & Kay 1991). It is likely that the medium sized home-ranges in November 1991 and February 1992 were a compromise between the need to forage widely for food and the need to stay close to reliable cover and water. In April and July 1992 female home-range size increased probably because cooler temperatures meant sows did not have to remain close to cover and water and could forage more widely to satisfy their nutritional requirements. In November 1992 home-range size fell again as temperatures rose and the requirement for water and cover rose. Home-range size did not rise again with cooler conditions in April and July 1993 because pasture biomass had risen dramatically in all habitats and there was no need to forage widely to satisfy nutritional demands.

Unlike the analysis of home-range size there was no significant difference between the sexes in distances moved. The reason distance moved decreased with increasing pasture biomass in shrubland is probably the same reason that home-range size decreased with increasing pasture biomass in shrubland. With increasing pasture biomass in shrubland pigs would not have to travel as far to find sufficient food to satisfy their hunger.

Pigs are more active at night during the hotter weather than during the cooler weather as can be seen from Figure 2.17. However even in the coolest weather pigs tended to be most active after dark. Nocturnal activity by feral pigs and wild boar is apparent in other studies in more temperate climates (Singer *et al.* 1981, McIlroy 1989, Saunders & Kay 1991). Graves (1984) has suggested that pigs are facultatively nocturnal due to hunting pressure and when not hunted revert to being fully diurnal. The pronounced increase in distance moved immediately after sunset is probably when pigs are moving from their bedding places to feed and drink. The ability to switch from nocturnal to diurnal activity depending on conditions is not shared with some other large herbivores which tend to be more rigidly diurnal or crepuscular (Jarman & Jarman 1973).

The lack of significant difference in body weight between the sexes is unusual as most other studies show boars to be clearly larger than sows (Oloff 1951, Sludskii 1956, Dzieciolowski *et al.* 1990, Cayley 1993). However, the difference in weights of male and female feral pigs studied by Barrett (1978) varied from boars being 5.3% larger in summer when conditions were harshest, to only 1.4% larger in winter. A possible explanation for the lack of significant differences in weights between the sexes at Nocoleche would be if there was disproportionately higher mortality for smaller females than smaller males leaving a higher percentage of larger females. This is possible as lactation is a severe burden on the energetic reserves of feral pigs (Barrett 1978) and may be more severe on smaller sows as resistance to starvation tends to increase with body size (Linstedt & Boyce 1985).

The results of the analysis of body weight must be interpreted with caution. In this analysis body weight is not used as an index of condition but the change in mean body weight is assumed to index increasing or decreasing access to food. As woodland was a little preferred habitat the significance of its pasture biomass in the regression of body weight is difficult to explain. An explanation for the significant effect of temperature is more obvious considering its importance in explaining habitat utilisation and female home-range size. When temperatures are high pigs are restricted to areas with dense cover and close water. This prevents them from foraging more widely in other habitats and so they can not maximise their intake of food. A further complication is that high ambient temperatures depress the appetite of domestic pigs (Heitman & Hughes 1949). If this is the case with the feral pigs at Nocoleche, it may act to exacerbate any summer food shortage.

The following paragraph summarises how habitat use, home-range size, distance moved, and body weight interacted with the environmental variables over the 18 month study. In November 1991 conditions were hot and food sparse in most habitats. Pigs were nocturnal, moved substantial distances probably in search of sparse food within a home-range restricted mostly to riverine woodland and had low body weights. The pattern is similar in early 1992 but with an increase in distances moved. In both November 1991 and February 1992 movement rates peaked shortly after sunset as did proportional use of riverine woodland probably as a result of pigs moving to the Paroo River to drink. In April 1992 with decreasing temperature the pressure to find dense cover was relaxed and while still primarily nocturnal pigs become more diurnal, often being observed asleep in full sunshine during cool days. Food was still relatively sparse so home-ranges in females expanded to their maximum to search for food without the constraint to return to denser cover. By July 1992 pigs had become highly diurnal and were not constrained by the need to return to dense cover. Increasing pasture biomass caused shrubland to become the most preferred habitat despite low overall pasture biomass compared to riverine woodland. At this time mean body weight was the highest since the start of the study. With increasing temperature in November 1992, pigs were once again confined to areas of dense cover even though there was more pasture than ever in the shrublands. Female home-range size declined with the requirement to return to cover, but pigs remained substantially diurnal despite the high day time temperatures. This was probably because while conditions were hot during the November 1992 tracking session, they were also overcast, reducing radiant heat load. Body weight declined from its winter peak. In April 1993 pigs still showed a preference for riverine woodland. Body weight increased with increasing food supply while female home-range remained small, sows not having to forage widely to meet their nutritional requirements. In July 1993 shrubland became the preferred habitat while distance moved and female home-range size reached a minimum for the study and body weight a maximum in response to abundant feed.

The patterns observed in habitat selection home-range size, distance moved and the concomitant variation in body weight are best interpreted in a central place foraging context. To a pig a central place is an area of dense cover that it returns to after foraging, not only for protection from high temperature but concealment during its prolonged sleep period. Thus the dispersion of central places determines where pigs will spend a substantial fraction of their time. The density of "central places" is greatest in riverine woodland and lowest in ephemeral swamps, so that while an individual pig can find all its "central place" requirements in the habitat with the least cover, more central places are available in the riverine woodland, hence most pigs seek shelter there.

There are several implications of these findings for the broad scale abundance and distribution of feral pigs in inland Australia. Choquenot (1994) found that the proportion of black soil habitat (riverine woodland, woodland) influenced the rate of decrease in feral pig populations during drought. The higher the proportion of soil the lower the rate of decrease. Riverine woodland provides a refuge as food abundance is higher during drought and protection from high temperatures is greater during summer. Therefore the more of this habitat the lower the drought induced mortality rate.

Habitat preference has the potential to influence disease transmission in two main ways. First by altering the dispersion of the hosts and second by altering the survival probability of the pathogen outside its host. If there is a seasonal change in habitat preference from a more broadly available habitat such as shrubland to a more concentrated habitat such as riverine woodland, then habitat specific density should increase even if overall density does not. As density of susceptible animals is a key parameter in the likelihood of the establishment of a disease this could mean an epidemic will have a much higher probability of becoming established when animals aggregate in smaller habitats. There is evidence for this in the increased incidence of FMD in impala *Aepyceros melampus* during dry season aggregations in Kruger National Park, South Africa (Plowright 1988).

That pig abundance increases with rainfall driven increases in pasture biomass is established (Giles 1980, Choquenot 1994). However, if pigs react to increasing pasture biomass during cool conditions by occupying the more extensive shrubland habitat then their habitat specific density will decrease possibly countering any effect of increasing overall density.

Current models of FMD in feral pigs (Pech & Hone 1988, Pech & McIlroy 1990) assume random movement by animals and hence contact rate based on density. If as seems more likely, animals are either attracted or repelled by one another, then contact rate may become independent of density. Feral pigs can form substantial sized groups of up to 50 individuals in other parts of Australia (Dexter pers. obs.) but pigs were rarely seen in large groups at Nocoleche.

On a finer temporal scale daily concentration of pigs at watering points may be particularly important in disease transmission especially if they are highly synchronised as seems possible immediately after sunset in November 91. For shrubland habitat where water is concentrated in earth tanks rather than spread out along the river the concentration of pigs at watering points may be very high.

As described in the introduction, the FMD virus is sensitive to low humidity, which is characteristic of the semi-arid rangelands most of the time. This means that long distance wind born transmission is unlikely most of the time. Humidity will probably vary according to microhabitat so that more humid microhabitats such as *M. florulenta* thickets could be the most likely place for FMD transmission.

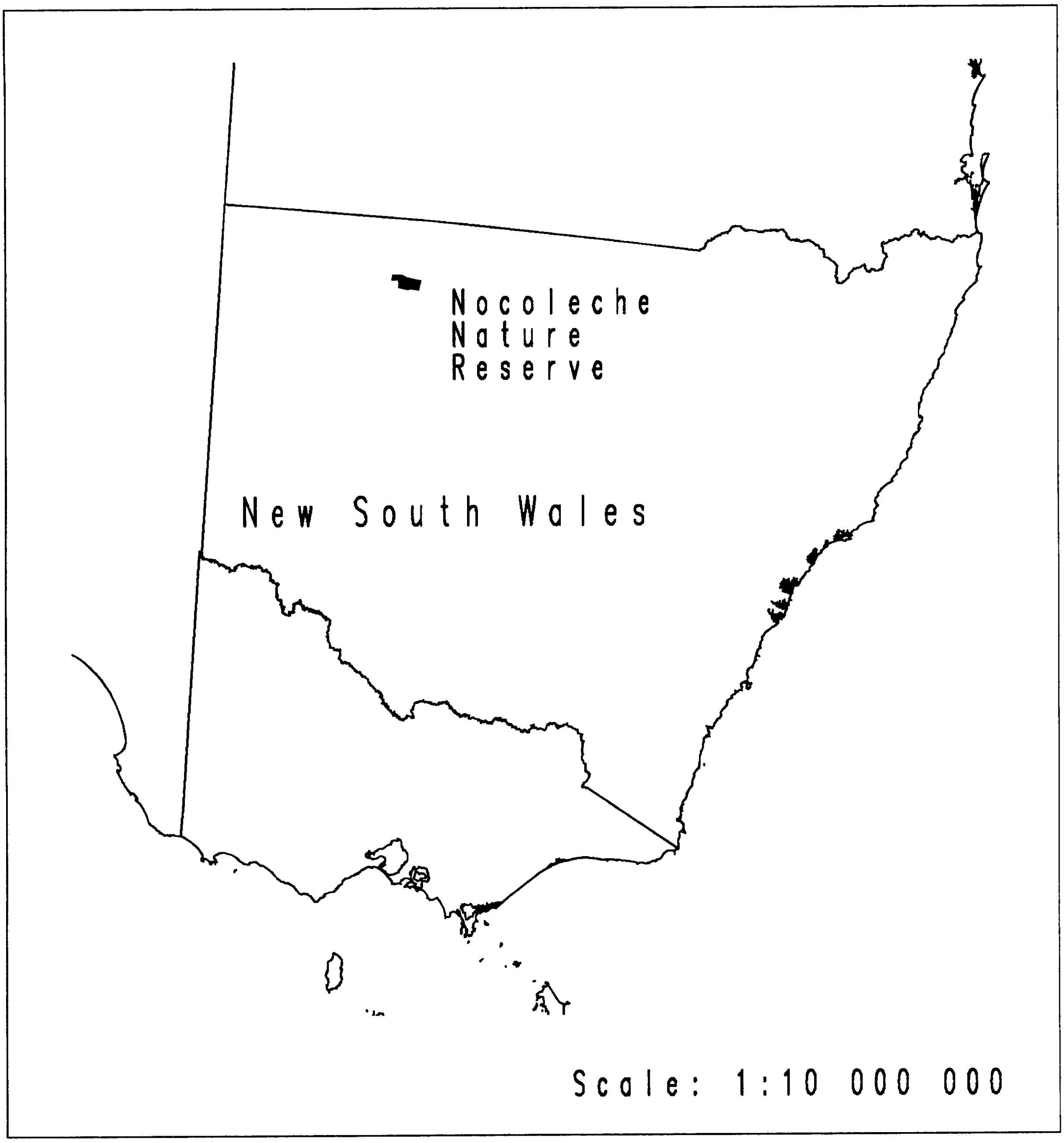


Figure 2.1 Location of feral pig study site, Nocoleche Nature Reserve, New South Wales, Australia.

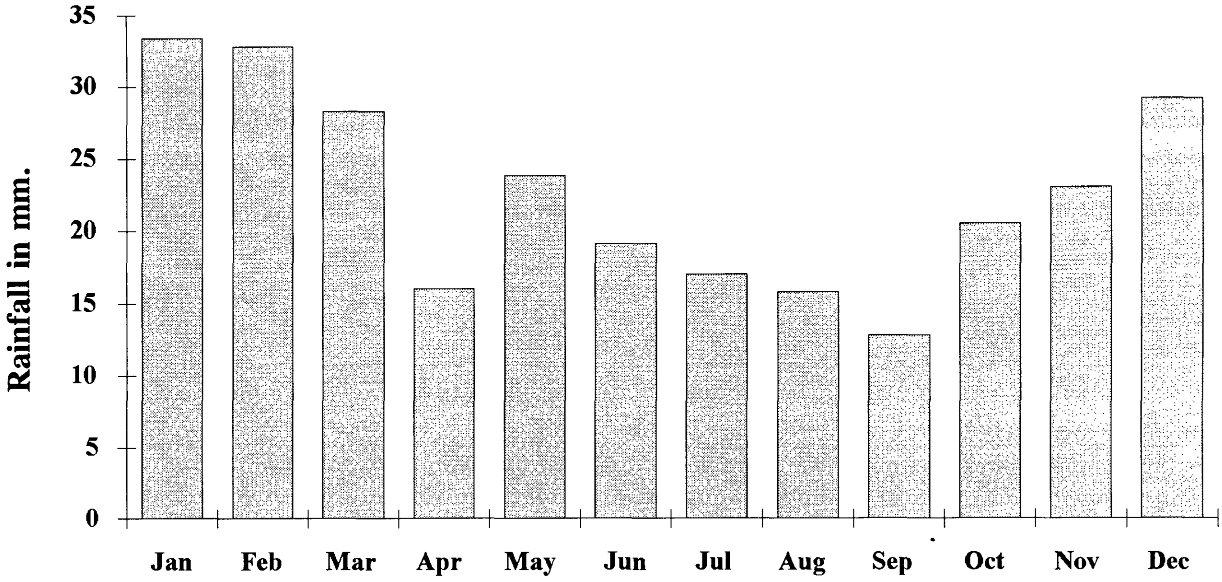


Figure 2.2 Mean monthly rainfall for Wanaaring, New South Wales.

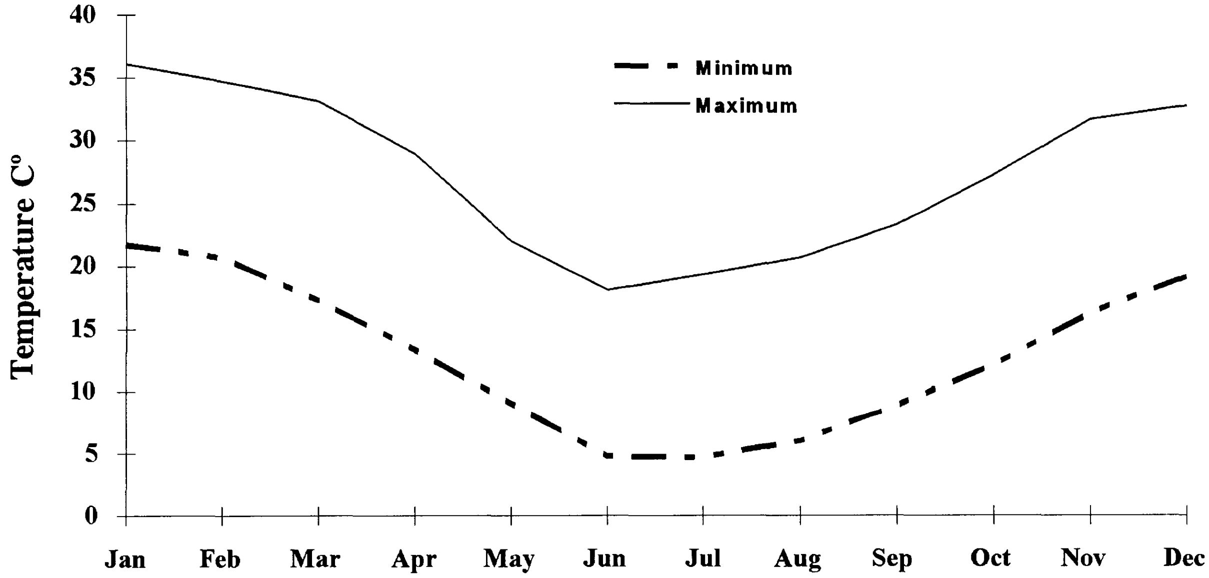


Figure 2.3 Mean maximum and minimum temperature for Wanaaring, New South Wales.

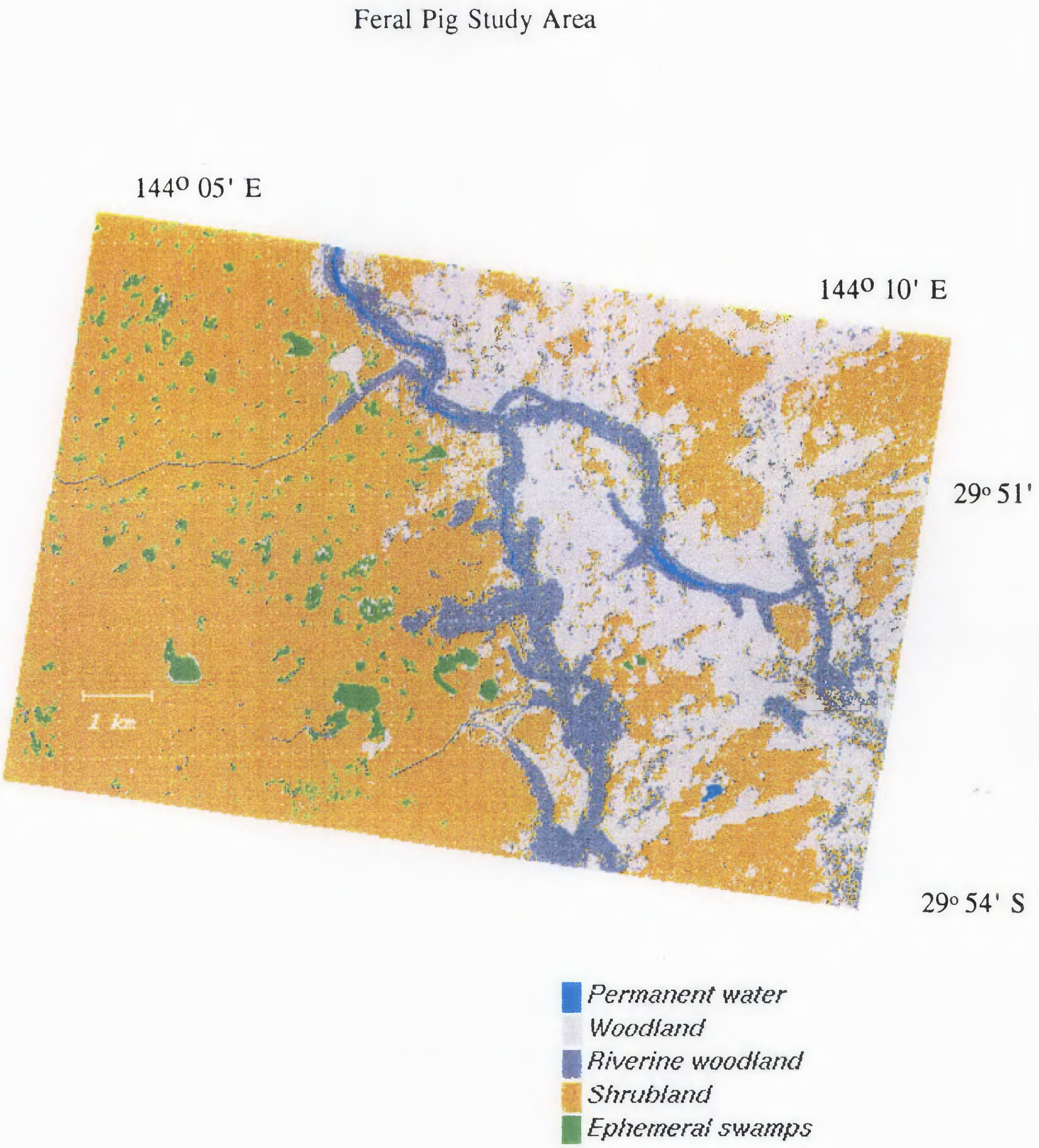


Figure 2.4 Distribution of habitats in study area, Nocoleche Nature Reserve.

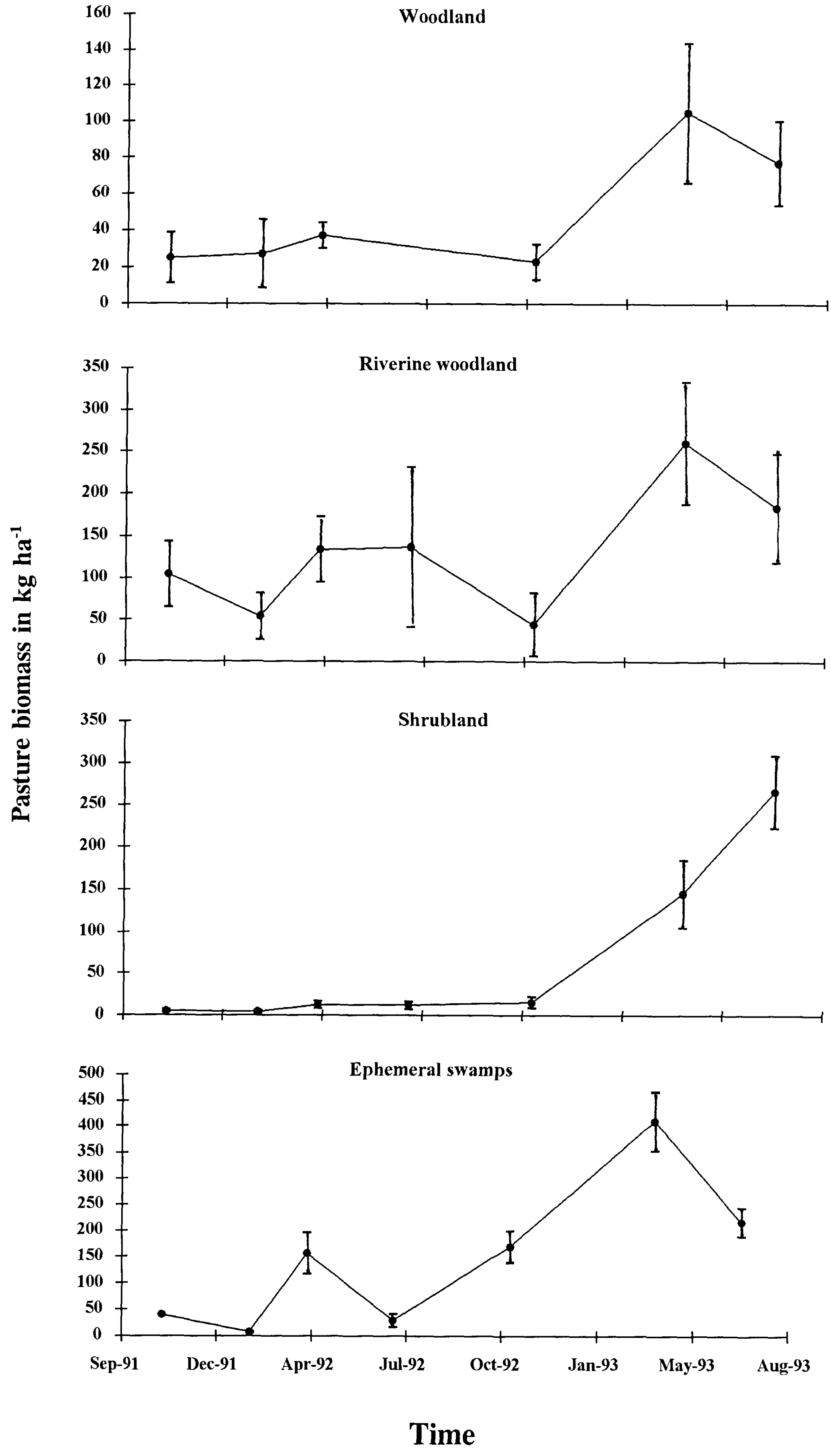


Figure 2.5 Change in pasture biomass kg ha^{-1} $\pm$ ISE in woodland, riverine woodland, shrubland and ephemeral swamp.

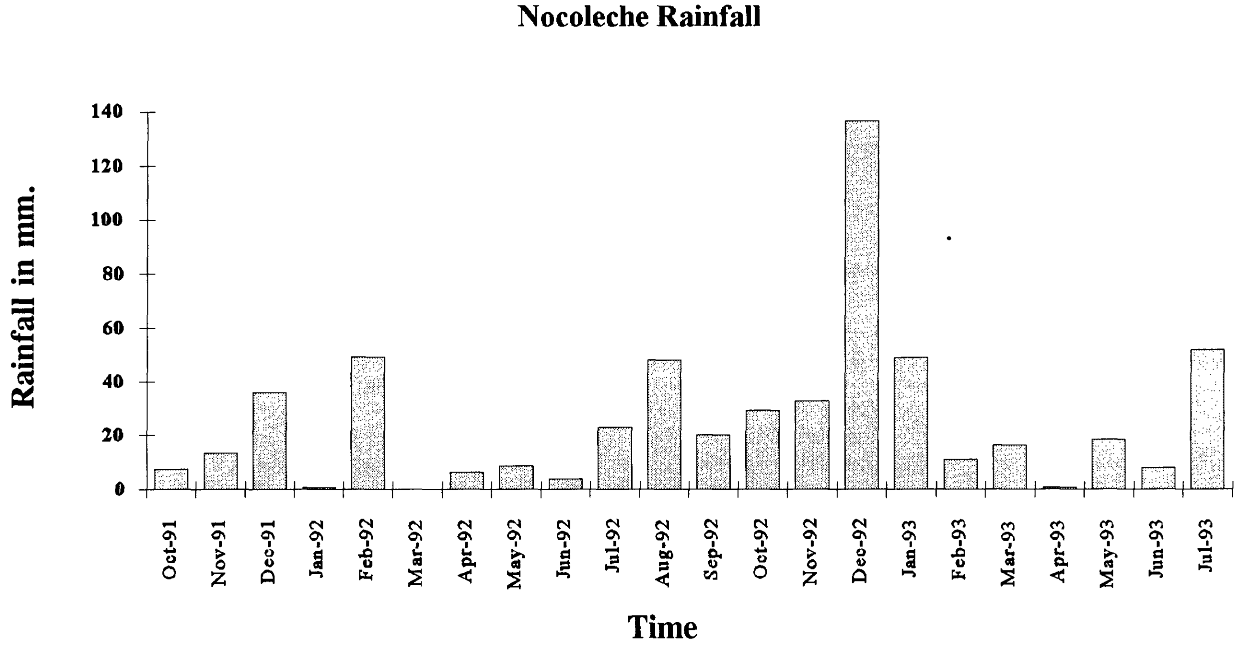


Figure 2.6 Monthly rainfall during course of study: October 1991 to July 1993.

Feral Pig Locations November 1991

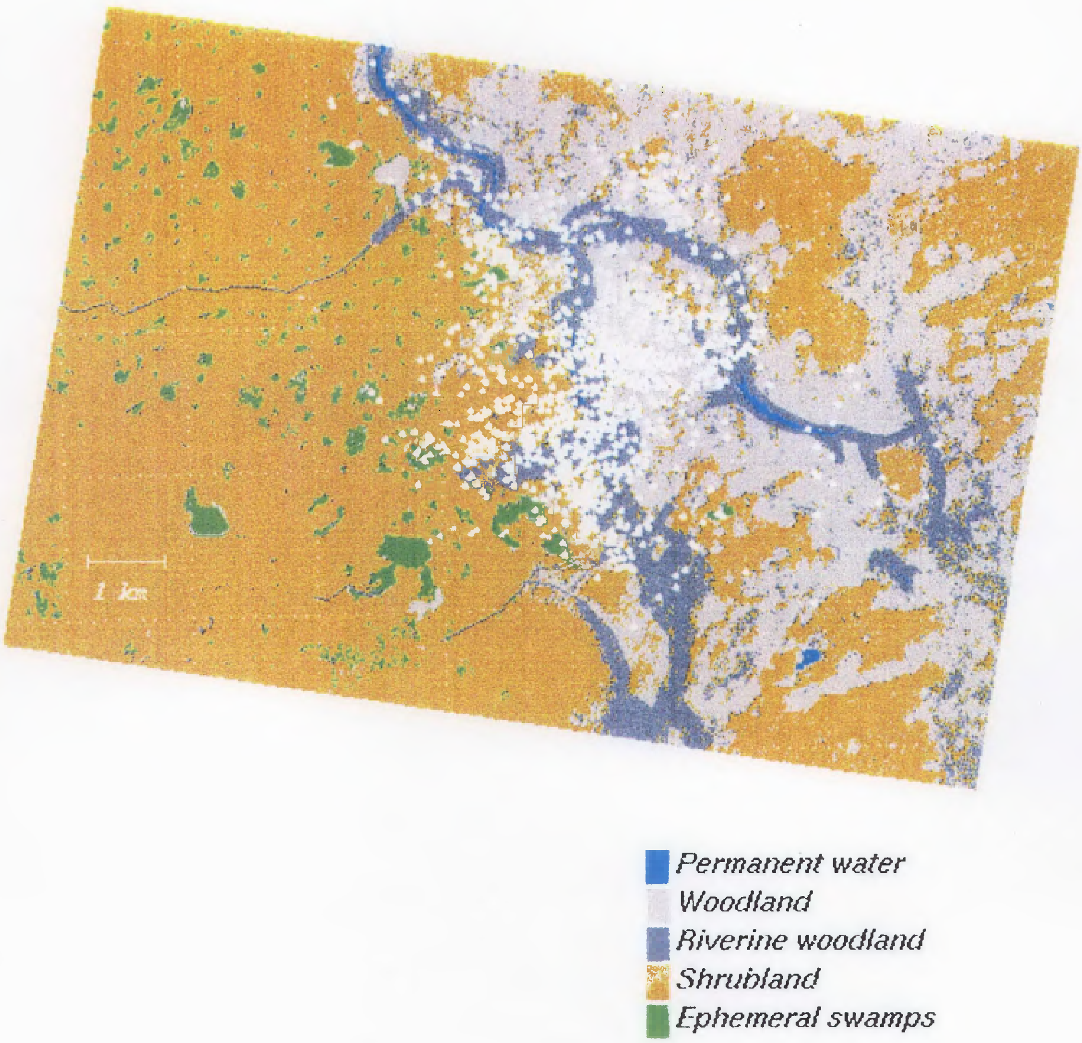


Figure 2.7. Distribution of radio-telemetry locations of feral pigs at Nocoleche Nature Reserve November 1991.

Feral Pig Locations February 1992

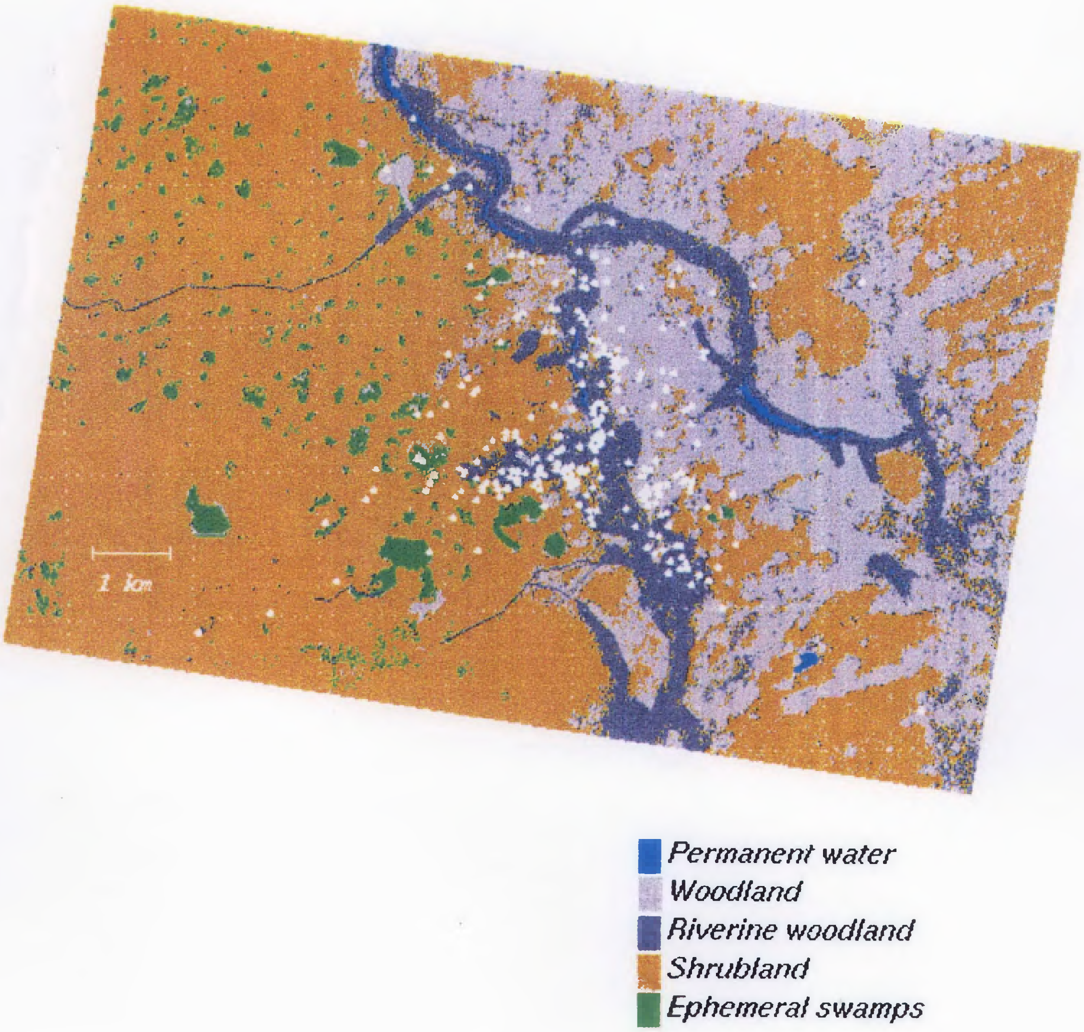
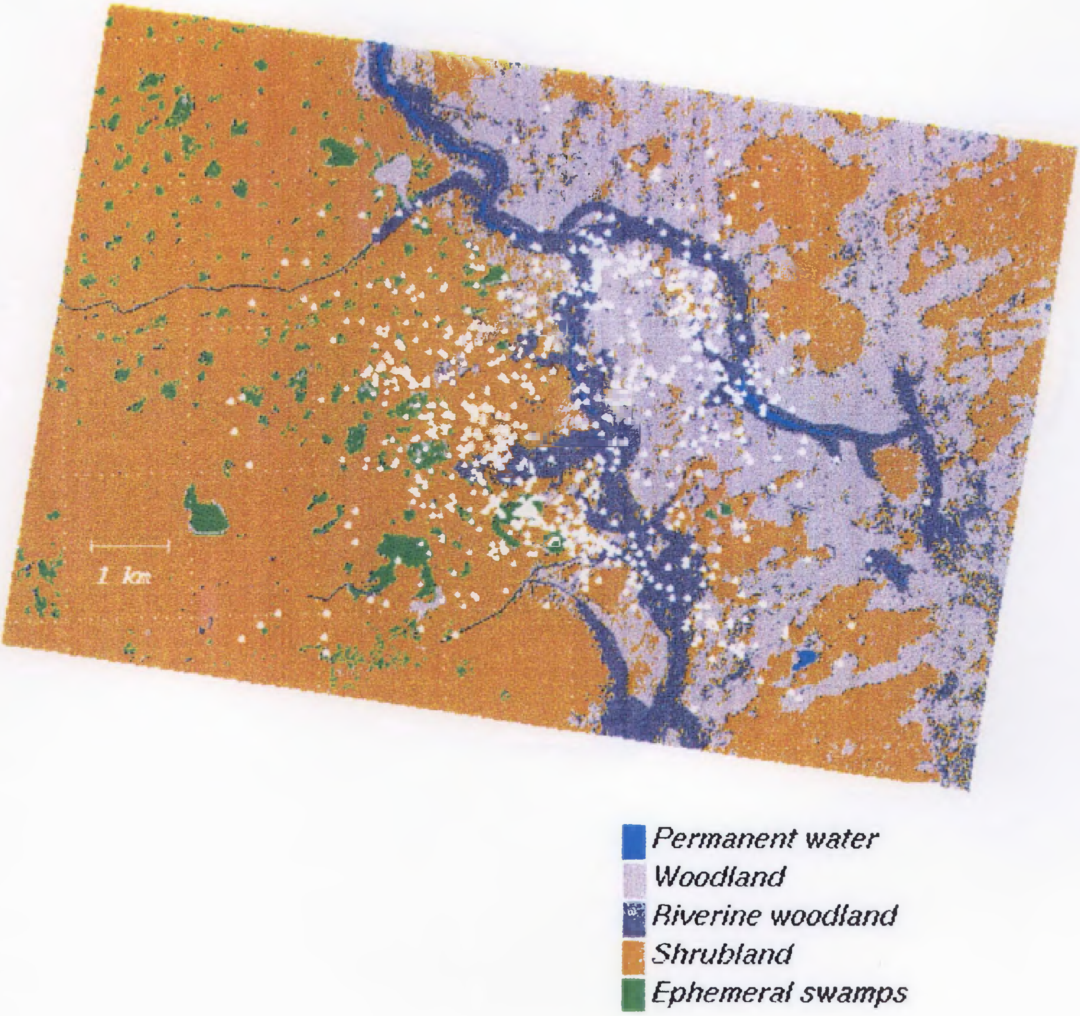


Figure 2.8. Distribution of radio-telemetry locations of feral pigs at Nocoleche Nature Reserve February 1992.



Feral Pig Locations April 1992

Figure 2.9. Distribution of radio-telemetry locations of feral pigs at Nocoleche Nature Reserve April 1992.

Feral Pig Locations July 1992

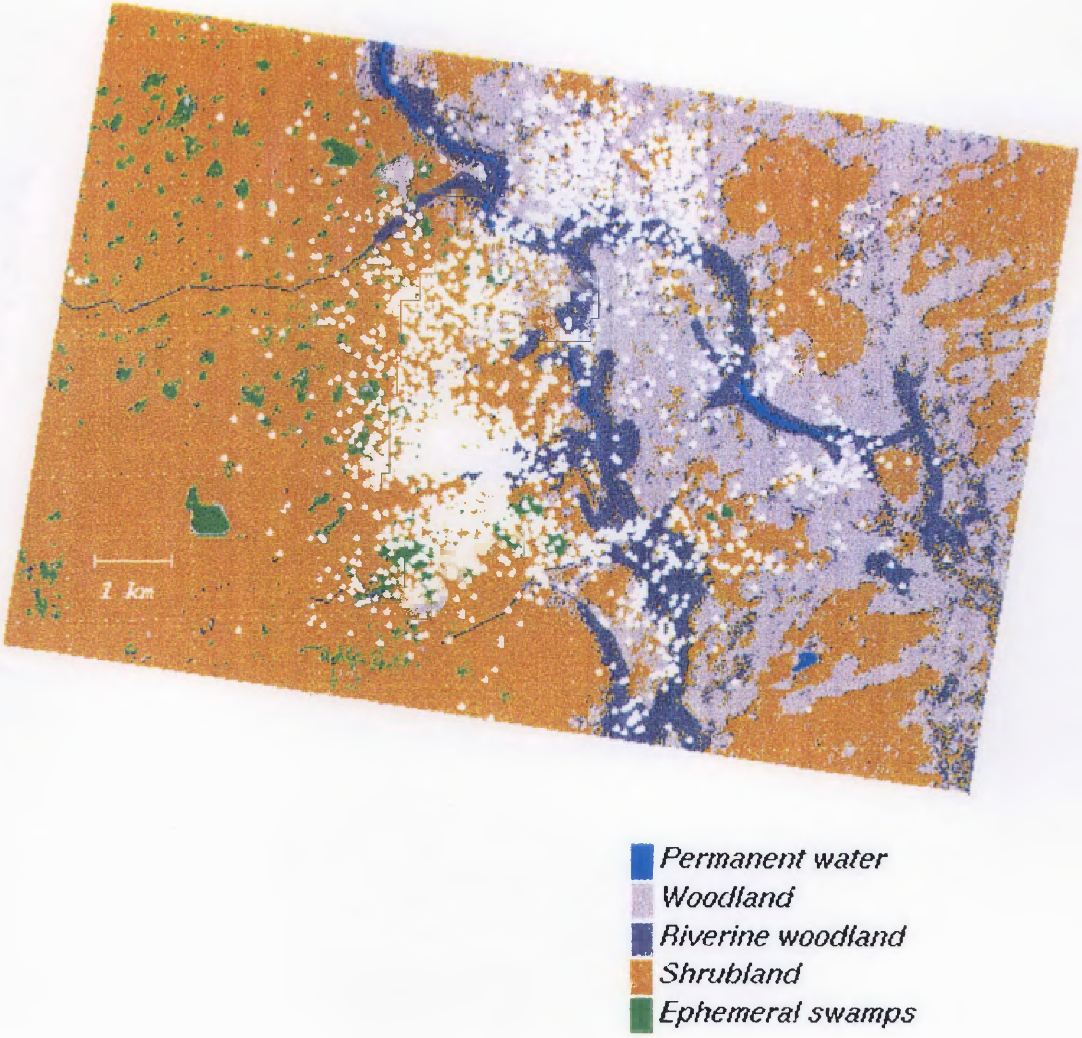
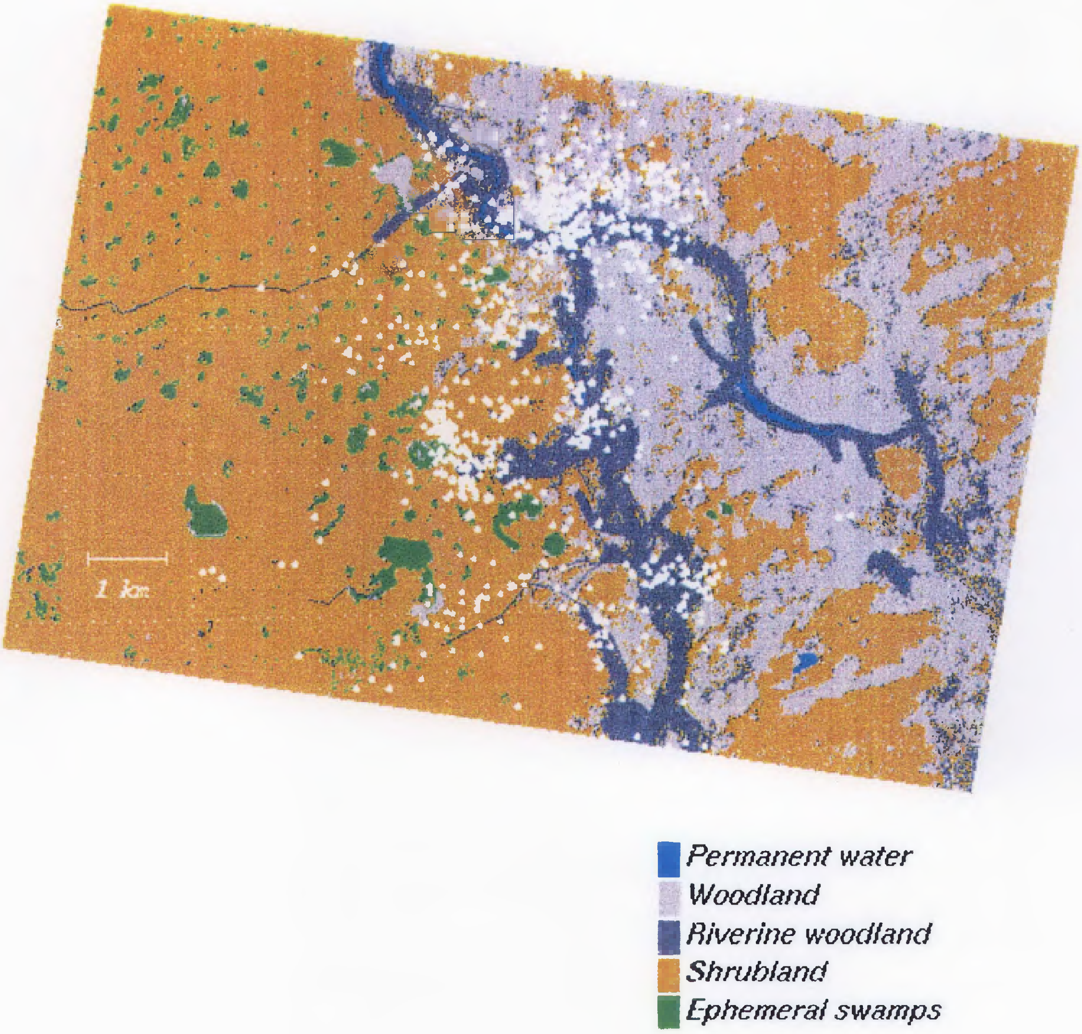


Figure 2.10. Distribution of radio-telemetry locations of feral pigs at Nocoleche Nature Reserve July 1992.



Feral Pig Locations November 1992

Figure 2.11. Distribution of radio-telemetry locations of feral pigs at Nocoleche Nature Reserve November 1992.

Feral Pig Locations April 1993

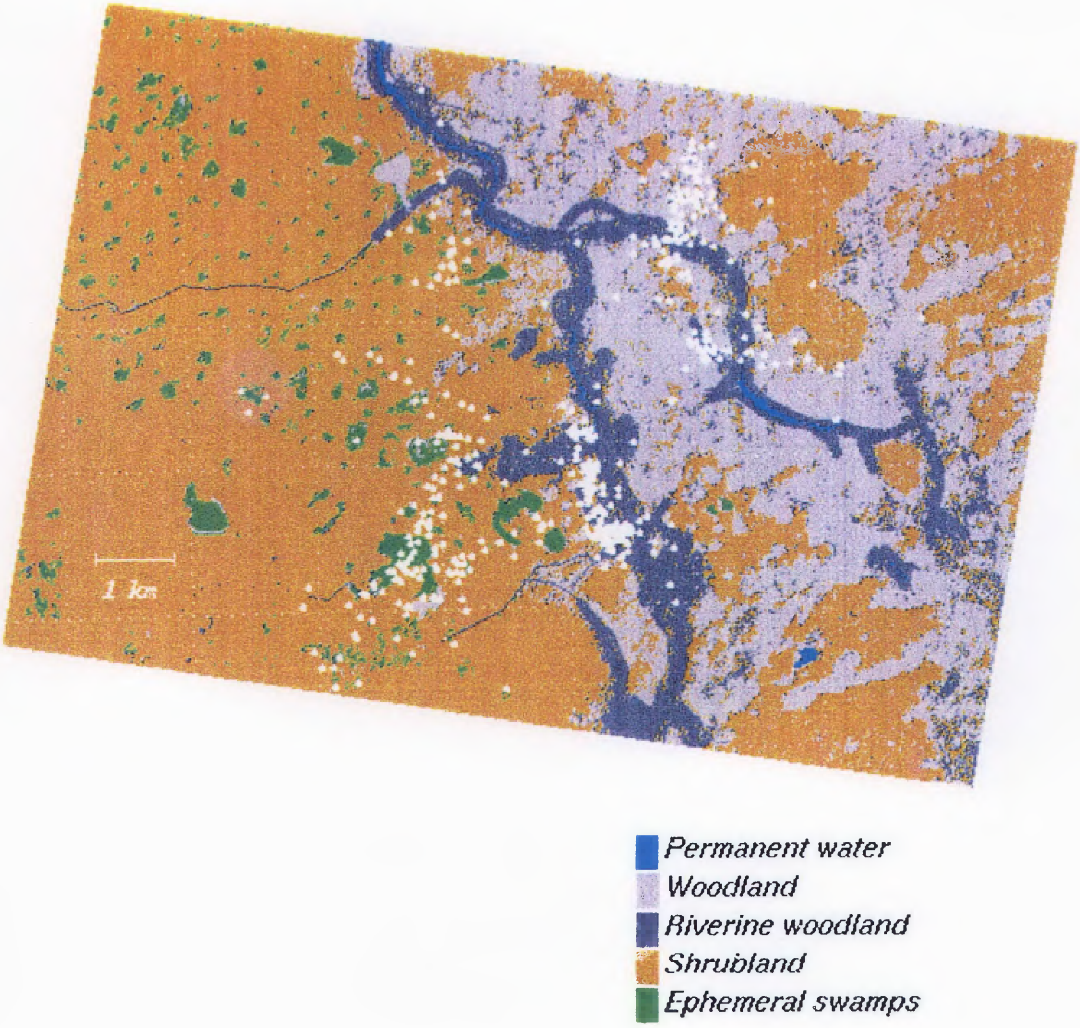


Figure 2.12. Distribution of radio-telemetry locations of feral pigs at Nocoleche Nature Reserve April 1993.

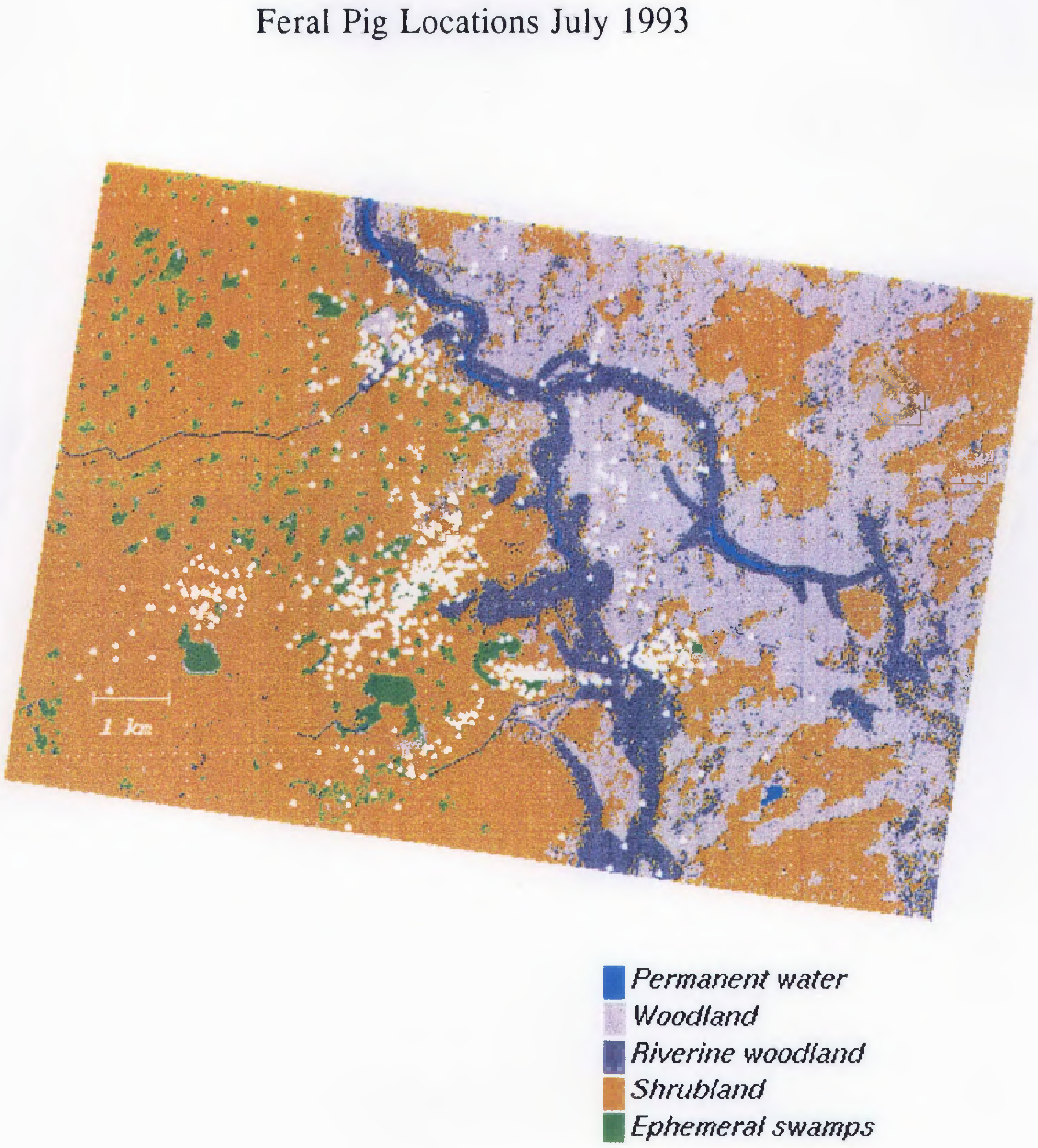


Figure 2.13. Distribution of radio-telemetry locations of feral pigs at Nocoleche Nature Reserve July 1993.

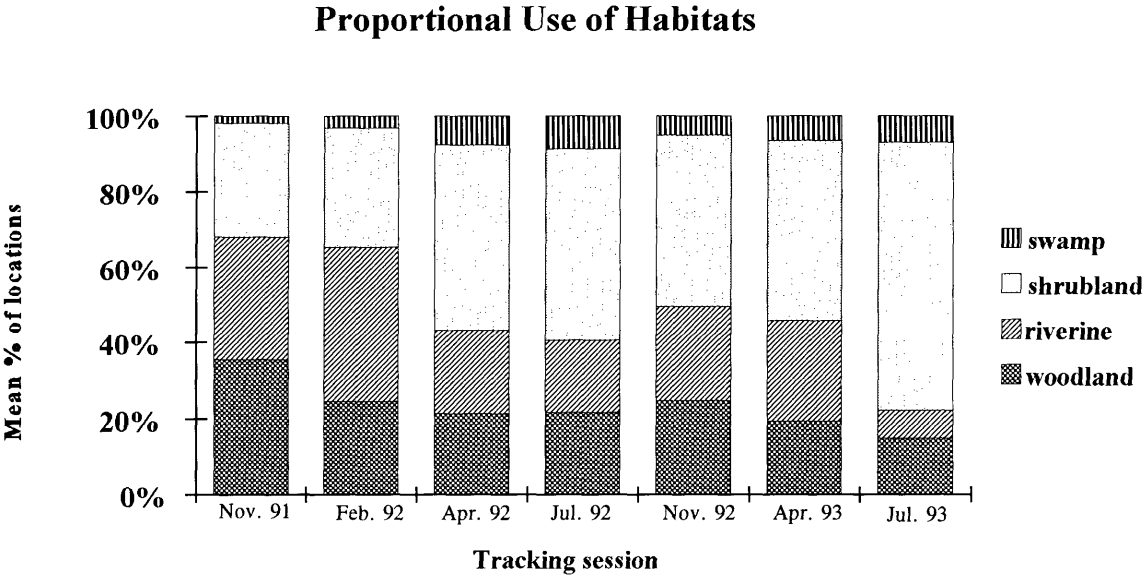
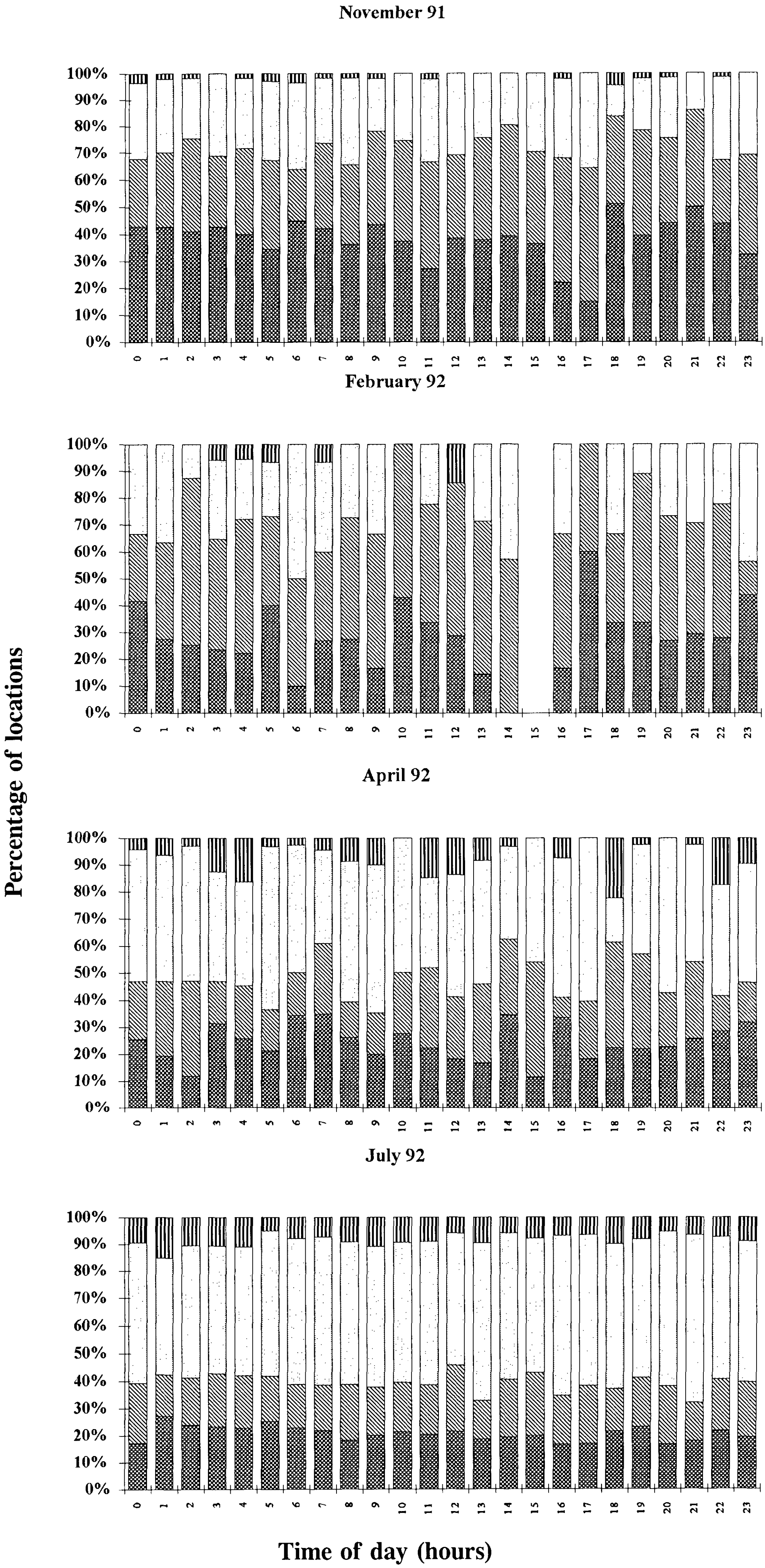


Figure 2.14 Change in proportional use of habitats for all pigs combined. Availability of habitats: woodland 30.2%, riverine woodland 15.1%, shrubland 51.4%; and ephemeral swamps 3.3%.


November 91
February 92
April 92
July 92
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23
Percentage of locations
Time of day (hours)

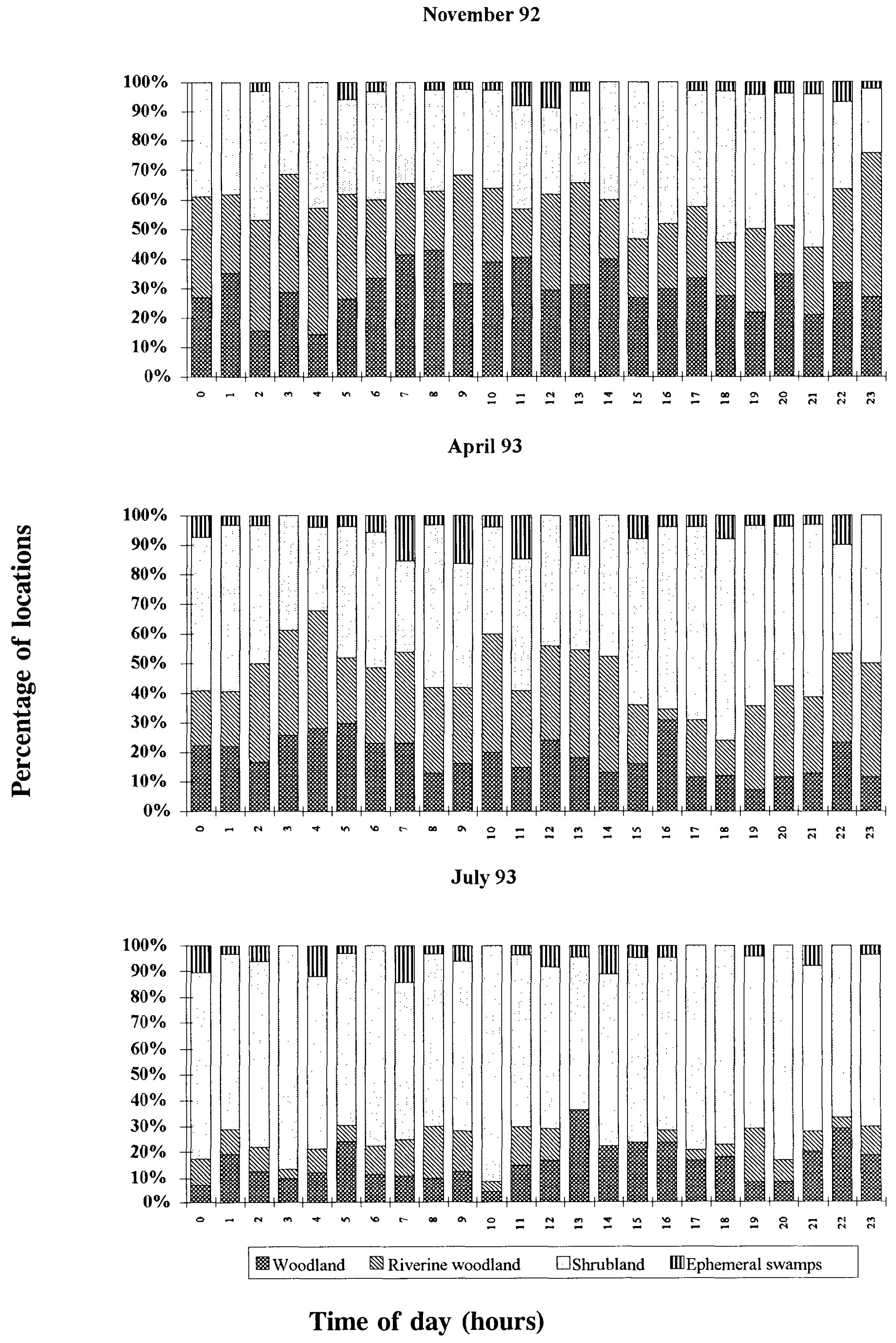
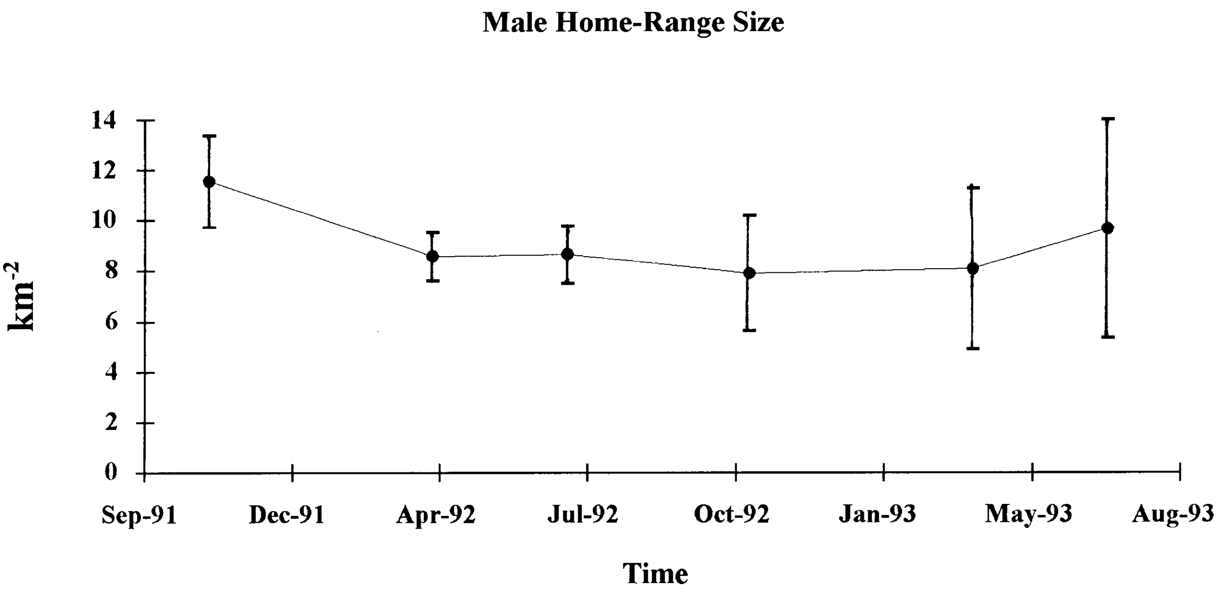
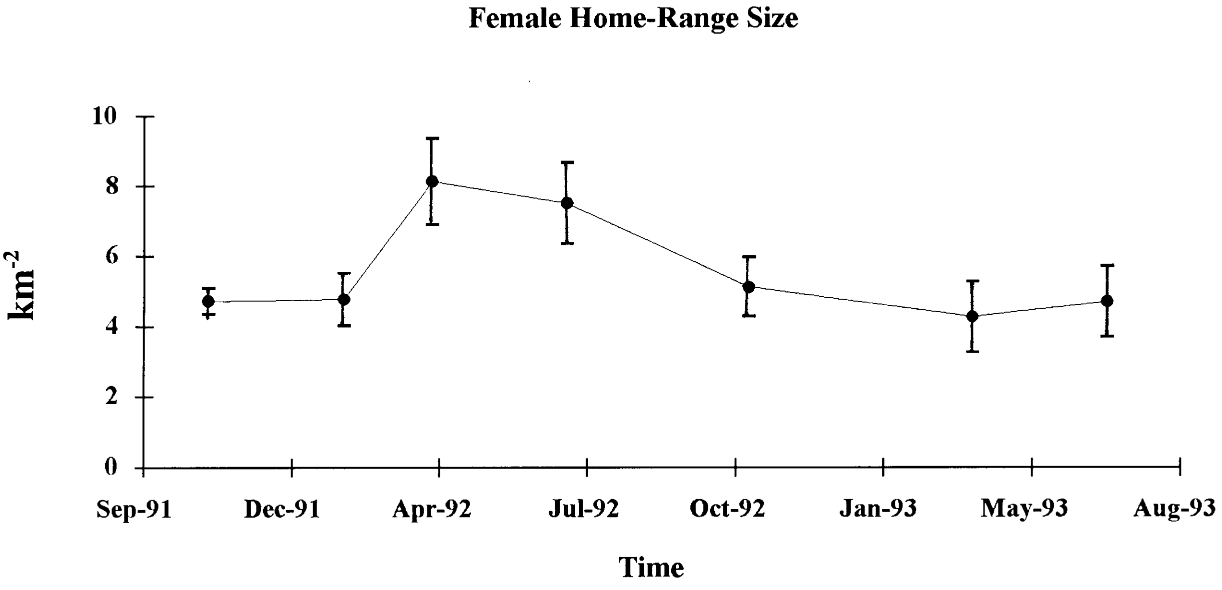


Figure 2.15 Diel variation in percentage of locations in woodland, riverine woodland, shrubland, and ephemeral swamps. November; February; sunrise 5 to 6, sunset 2000 to 2100, April; sunrise 600 to 700, sunset 1800 to 1900, July; sunrise 700 to 800, sunset 1700 to 1800. Too few records (2) to determine proportional use for 15, Feburary 1992.



Male Home-Range Size



Female Home-Range Size

Figure 2.16 Change in home range size in km^2 ± 1SE for male and female pigs.

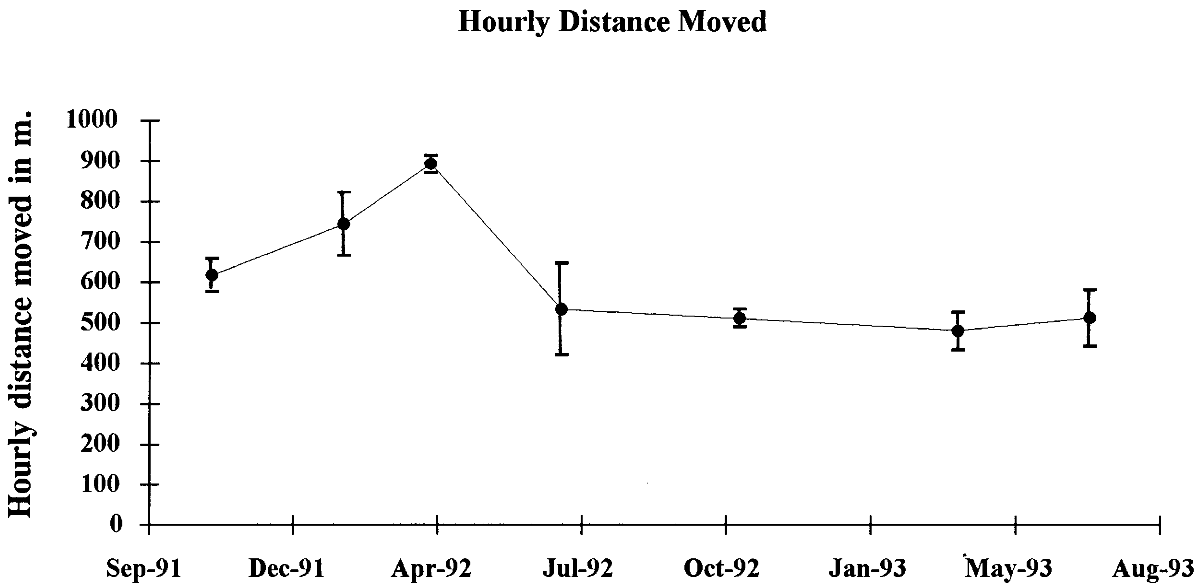
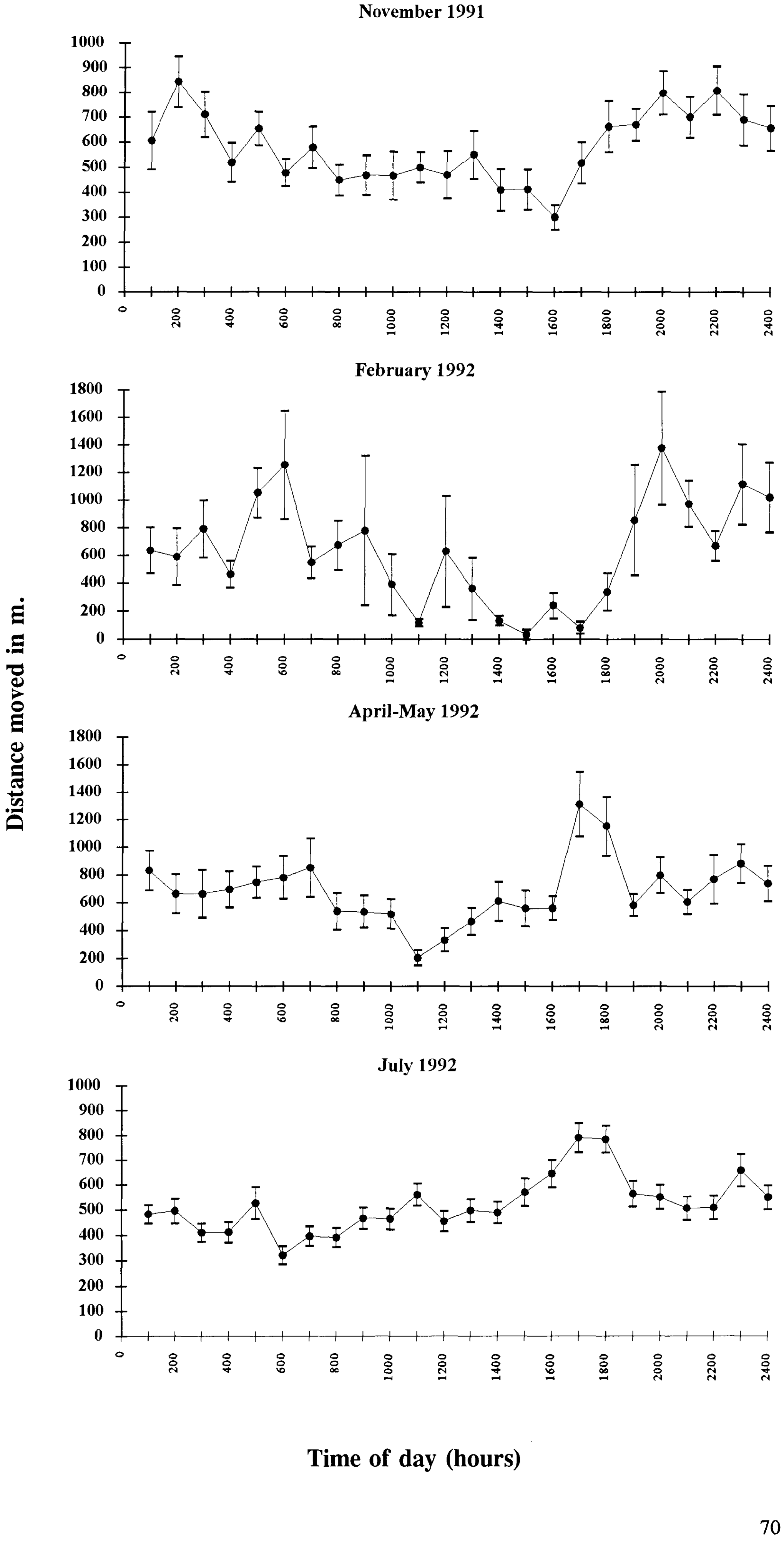


Figure 2.17 Change in mean hourly distance moved in metres ± 1SE.


November 1991
February 1992
April-May 1992
July 1992
Distance moved in m.
Time of day (hours)
1000
900
800
700
600
500
400
300
200
100
1800
1600
1400
1200
1000
800
600
400
200
0
0
200
400
600
800
1000
1200
1400
1600
1800
2000
2200
2400

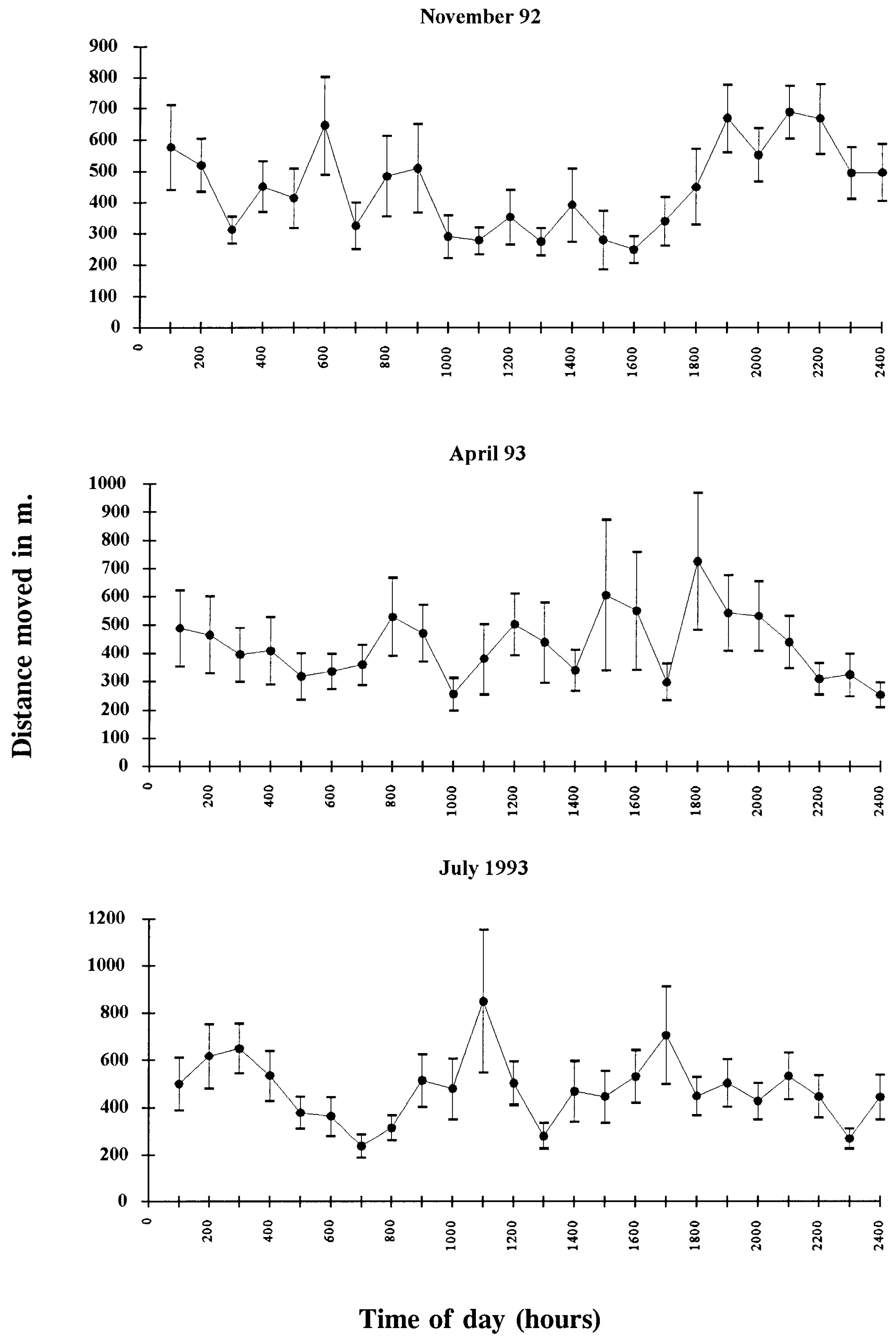


Figure 2.18 Diel variation in mean hourly distance moved by feral pigs ± 1SE. November; February; sunrise 500 to 600, sunset 2000 to 2100, April; sunrise 600 to 700, sunset 1800 to 1900, July; sunrise 700 to 800, sunset 1700 to 1800.

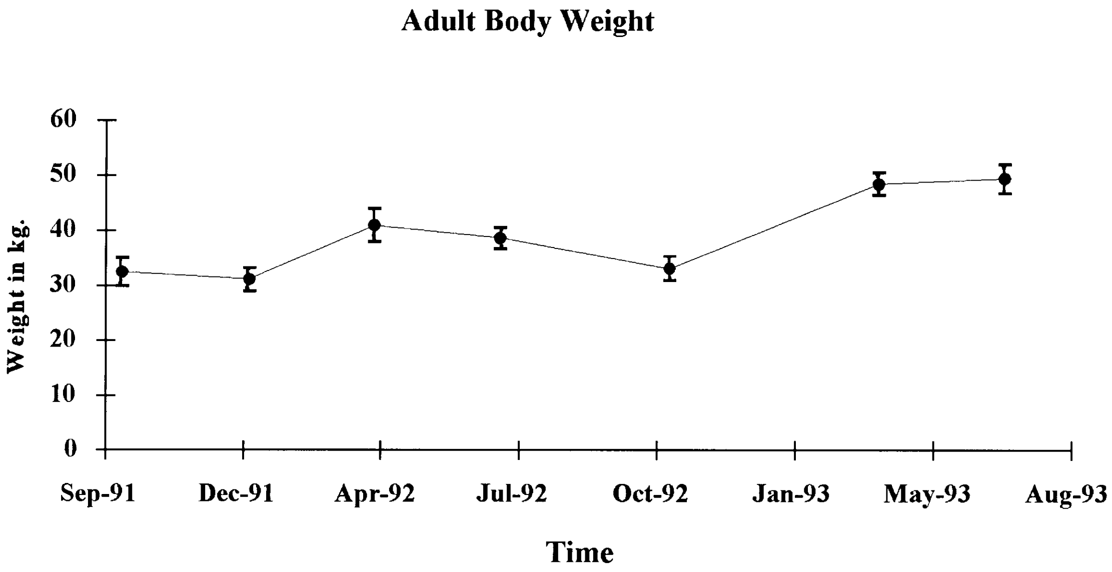


Figure 2.19 Change in mean adult (> 1 year old) body weight in kilograms ± 1SE.